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An age-structured Bayesian population model for St. Lawrence Estuary beluga (*Delphinapterus leucas*)

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

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ABSTRACT

The St. Lawrence Estuary (SLE) beluga population was depleted by intensive hunting and declined from 5000-10000 individuals at the end of the 1800's to a few hundreds in 1979 when it was afforded protection by the Fisheries Act. The low abundance estimate obtained from the photographic survey conducted in 2009 and the high mortalities observed in 2008, 2010 and 2012 raised concerns as to the status of SLE beluga. An age-structured hierarchical Bayesian model was used to describe the population dynamics of SLE beluga and trends in population abundance. The model included information on population abundance and proportion of young (0-1 year-old calves) obtained from 8 photographic aerial surveys flown between 1988 and 2009, and mortalities of newborns and older individuals documented by a carcass monitoring program maintained from 1983 to 2012. Results suggest that the population was stable or slightly increasing from the end of the 1960s until the early 2000s when it numbered approximately 1000 beluga. The population then started to decline to 889 individuals (95%CI 672-1167) in 2012. To explain this decline, the model suggests important changes in population dynamic parameters and age structure, moving from a stable period (1984-1998) characterized by a 3-year calving cycle, a population composed of 42% of immature individuals and 7.5% newborns, to an unstable situation (1999-2012) showing a 2-year calving cycle, and a declining proportion of newborns and immatures (respectively 6% and 33% in 2012), associated with a high newborn mortality. Independent abundance indices and observations of year-to-year variation in calf production and age-structure show similar trends to those predicted by the model, thus increasing our confidence in its conclusions. The lack of recovery, high overall adult mortality (6%) and highly variable newborn survival could indicate a population limited by resources in its environment, and thus particularly sensitive to climate variability and cascading effects in the ecosystem.

Un modèle de population Bayésien structuré par âge pour le beluga (*Delphinapterus leucas*) de l'estuaire du Saint-Laurent

RÉSUMÉ

La population de beluga de l'estuaire du St. Laurent (ESL), a été décimée par une chasse intensive passant de 5000-10000 individus à la fin de des années 1800 à quelques centaines en 1979 lors qu'elle fut protégée en vertu de la *Loi sur les Pêches*. Le faible estimé d'abondance obtenu par le relevé photographique effectué en 2009 et les fortes mortalités observées en 2008, 2010 et 2012 ont soulevé des préoccupations quant au statut du béluga de l'ESL. Un modèle Bayésien hiérarchique structuré par âge a été utilisé pour décrire la dynamique de la population de bélugas de l'ESL et examiner l'évolution de ses effectifs. Le modèle inclut des données sur l'effectif de la population et sur la proportion de jeunes obtenus à partir de 8 inventaires aériens photographiques réalisés entre 1988 et 2009, et les mortalités de nouveau-nés et d'individus plus âgés documentées à travers un programme de suivi des carcasses couvrant la période 1983 à 2012. Les résultats suggèrent que la population était stable ou en légère croissance de la fin des années 1960 jusqu'au début des années 2000. Estimée alors à environ 1000 bélugas, elle aurait commencé à décliner depuis lors jusqu'à atteindre 889 individus (95%IC 672-1167) en 2012. Pour expliquer ce déclin, le modèle suggère d'importants changements dans les paramètres de la dynamique de la population et dans sa structure d'âge, passant d'une période stable (1984-1998) caractérisée par un cycle reproducteur de 3 ans, une population composée de 42 % d'individus immatures et 7,5 % de nouveau-nés, à une situation instable (1999-2012) montrant un cycle reproducteur de 2 ans, et une proportion décroissante de nouveau-nés et d'individus immatures (respectivement 6 % et 33 % en 2012) associée à une forte mortalité des nouveau-nés. Des indices d'abondance et des observations de la variation interannuelle de la production de veaux et de la structure d'âge provenant de sources indépendantes, montrent des tendances similaires à celles prédites par le modèle, renforçant notre confiance dans ses conclusions. L'absence de rétablissement, la forte mortalité adulte (6 %) et la survie très variable des nouveau-nés pourrait être les signes d'une population limitée par les ressources de son environnement, et de ce fait très sensible à la variabilité du climat et à ses effets indirects sur l'écosystème.

INTRODUCTION

The St. Lawrence Estuary (SLE) beluga (*Delphinapterus leucas*) population is located at the southernmost limit of the species range. It mainly occupies the SLE and move seasonally into the Gulf of St. Lawrence (Mosnier et al. 2010). Depleted by intensive hunting, this population declined from 5000-10000 individuals at the end of the 1800's (Reeves and Mitchell 1984, Hammill et al. 2007) to a few hundreds in 1979 when it was afforded protection by the *Fisheries Act* (Anonymous 1979, Lesage and Kingsley 1998). Listed as "endangered" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 1983 (Cook and Muir 1984), it received further protection under the *Species at Risk Act*. Its status was re-evaluated as "threatened" in 2004 (COSEWIC 2004). Despite the absence of hunting and the application of various protective measures, the population has failed to recover and was generally considered stable at around 1100 individuals (Gosselin et al. 2007, Hammill et al. 2007). The low population size estimate obtained from the photographic survey conducted in 2009 (Gosselin et al. 2014) and the high mortalities observed in 2008, 2010 and 2012 (Lesage et al. 2014) raised concerns as to the status of SLE beluga. Based on the best available information, we developed a Bayesian population model designed to describe the dynamics of this population and to provide insights into current population trends.

MATERIAL AND METHODS

An age-structured hierarchical Bayesian model was used to describe the population dynamics of the SLE beluga. The model was fitted to four datasets: 1) population abundance estimated from 8 photographic aerial surveys flown between 1988 and 2009, 2) proportion of young (defined below) obtained from the same surveys, 3) the number of dead newborns and 4) the number of dead beluga aged 1 year-old and older, both documented by the carcass monitoring program during the 1983-2012 period. The model also incorporated the mortality due to hunting for the period 1913-1960 (Laurin 1982 in Reeves and Mitchell 1984).

The use of a hierarchical Bayesian model allowed separating the population dynamics process (i.e. the variability due to natural changes in the population dynamics parameters) from the observation process (i.e. errors introduced during data collection and estimation procedures) (De Valpine and Hastings 2002).

THE POPULATION DYNAMICS MODEL PROCESS

General model form

The dynamics of the population was modelled by considering 11 age-classes grouped in 4 stages (Fig. 1a). Each stage was characterized by specific mortality and fecundity rates. The model assumed no density-dependence, and therefore the general equation for each cohort *a* (excluding newborns) in year *t* was:

$$N_{a,t} = N_{a-1,t-1} \times \exp(-Z_{s,t})$$

$$\text{and } \exp(-Z_{s,t}) = 1 - M_{s,t}$$

With $Z_{s,t}$ and $M_{s,t}$ the instantaneous and the annual mortality rate respectively, for the stage *s* in year *t*.

The first two classes were assigned to the stages "Newborn" and "Yearling" (Fig. 1a) describing respectively beluga born during the current year and individuals that survived their first year, but which are less than 2 years old. Both of these stages included individuals that are dependent on

their mother, but published references suggest that there are large differences in mortality rates between these two stages (Burns and Seaman 1985, Doidge 1990). In our model, newborn mortality (M1, Fig. 1a) was treated independently from other mortalities as it includes cause of death specific to this age class (e.g. peri-partum mortality). The mortality for yearlings (M2, Fig. 1a) was considered to be equal to twice the adult mortality (see section on priors).

The "Immature" stage included beluga aged from 2 to 7 years old (Burns and Seaman 1985) that have not yet begun to reproduce. This stage was subdivided into 6 age classes with the same mortality rate (M3, Fig.1a). This subdivision allowed the model to take into account the time lag that can exist between an event of high newborn mortality and its effect on productivity as individuals are recruited into the "Mature" portion of the population.

The "Mature" stage comprised individuals 8 years and older that can reproduce (Robeck et al. 2005, Suydam 2010, Lesage et al. 2014). It was composed of two classes that included 8- and 9-year-old beluga respectively and a third class that included beluga 10 years and older. The mortality rate for this stage was considered equal to that of the "Immature" stage (M3, Fig. 1a).

The beluga reproductive cycle is considered to last 3 years including gestation, (~14 months; Brodie 1971, Sergeant 1973, Burns and Seaman 1985) and lactation (12-18 months; Sergeant 1973, Burns and Seaman 1985). During this time, females are not available for reproduction. The model accounted for this by calculating the number of mature females (half of the mature population, assuming a ratio M:F of 1:1 [Vladykov 1944, Béland et al. 1988, Lesage et al. 2014]), that were not pregnant at the time of reproduction nor with a calf less than 1 year old. The model also considered that a female losing a calf during its first year was available for reproduction the following year, allowing for a shorter reproductive cycle as is sometimes observed (1 birth every 2 years versus 1 birth every 3 years; Vladykov 1944, Kleinenberg et al. 1964, Sergeant 1973, Burns and Seaman 1985). The pregnancy rate (Preg, Fig. 1a) was then applied only to the proportion *PropF* of mature females that were available (i.e. not pregnant, not with a calf less than 1 year old, or lost a calf during the previous year).

Therefore, the number of newborn in year *t* was:

$$N_{1,t} = \left(N_{8,t-2} + N_{9,t-2} + N_{10+,t-2}\right) \times 0.5 \times PropF_{t-2} \times Pregnancy_{t-1} \times (1 - M_{4,t-1})$$

Sub-models

This model was composed of two sub-models:

The first part, called the "adaptive part", used a deterministic version of the general model to estimate the population size and structure for the period 1913-1982 (Fig. 1b). During this period, mortality and pregnancy rates were fixed at a value corresponding to the median of the values estimated in the "fitting part" of the model (see below). Thus, all $M_{s,t} = M_s$ and all $Pregnancy_t = Preg$. As hunting activities occurred at least until 1960 (Reeves and Mitchell 1984), information on the number of beluga hunted each year was added to natural mortalities and the cohort equation became:

$$N_{a,t} = N_{a-1,t-1} \times (1 - M_s) - C_{a-1,t-1}$$

with *C* the hunting catches for each age *a* and year *t*

Hunting mortality at age was assumed to follow the same distribution as for beluga hunted in Nunavik from 2000 to 2010 (Doniol-Valcroze et al. 2011). The main objective of this part of the model was to let the population evolve conditionally to structuring elements such as the hunt and the population parameters estimated in the second part of the model, in order to minimize sensitivity to the population structure imposed in the initial year.

The second part of the model, called the "fitting part", used the stochastic version of the general model for the period 1983-2012 (Fig. 1c). Mortality and pregnancy rates were random variables (see section on priors) that could vary each year, as would be expected in a wild population. Data acquired through aerial surveys and the carcass monitoring program was used to inform the model during the period 1983-2012 and thus update the priors. The median values of each parameter (M_{nb}, M_{y1}, M_{adult}, Pregnancy; Fig. 1c) estimated for 1983-2012 were used as fixed values in the "adaptive part". Hunting mortality was assumed to be nil in this part of the model.

Initialisation

The age structure of the initial population is unknown. To initialise the model, we used the age structure of the beluga population wintering in the Bering Sea described in Burns and Seaman (1985). This population was hunted, as was the SLE beluga population in the first part of the 19th century, and was considered stable. This age structure was modified, however, to take into account that the estimation of ages in Burns and Seaman (1985) assumed deposition of two dentinal growth layers groups (GLGs) in tooth sections (Klevezal 1996) and not one as currently recognized (Stewart et al. 2006, Luque et al. 2007). A multiplicative term, α, estimated by the model, was applied to this age structure vector to control for the size of the initial population.

THE OBSERVATION PROCESS: AERIAL SURVEYS AND CARCASS MONITORING PROGRAM

Population abundance estimates and proportion of young

Population abundance estimates were obtained through 8 photographic strip transect surveys conducted in 1988, 1990, 1992, 1995, 1997, 2000, 2003, and 2009 (Kingsley and Hammill 1991, Kingsley 1993; Kingsley 1996; Gosselin et al. 2001; Gosselin et al. 2007; Gosselin et al. 2014). These surveys followed a systematic design with parallel transects lying perpendicular to the main axis of the St. Lawrence Estuary. The region from Bic or Rimouski to Petite-Rivière-Saint-François, recognized as the main summer area of the population (Mosnier et al. 2010), was flown in a single day. A count of beluga sightings was obtained via the examination of the photographic frames taken during the surveys by two readers following the method outlined by Stenson et al. (2000). The Saguenay River was also surveyed visually by helicopter or plane while the photographic survey was being conducted in the Estuary. The number of beluga and their positions were noted on both the upstream and downstream passes to remove duplicates. Final population estimates were obtained by including a correction to account for beluga that were undetected due to sun glare on photos (Kingsley 1996), an expansion factor ($f_1 = 2.021$) to compensate for the gaps between transects, another multiplying factor ($f_2 = 2.09$) to compensate for animals that were under the water when the aircraft passed overhead and finally adding the uncorrected Saguenay River count. The error around each abundance estimate was based on the serial differences in encounter rates among transects of each survey (Gosselin et al. 2007).

For each survey, young beluga were identified from the photos as individuals smaller than or equal to half the size of the nearest adults (Gosselin et al. 2014) and were assumed to be 0 and 1 year-old beluga (Lesage et al. 2014). The ratio of these young beluga relative to the total number of observed beluga was used in the model to estimate their proportion in the population (Gosselin et al. 2014). A potential difference in detection rate between young and adult beluga could result in uncertainty around those estimates. Although no information was available to define this uncertainty, we included an error term around these values in the model (see section on priors).

Carcass monitoring

The database from the carcass monitoring program (DFO 2007) contains information on the number of individuals found dead each year from 1983 to 2012 (n= 469; Lesage et al. 2014). However, some animals may sink, drift into the Gulf of St. Lawrence or be consumed by scavengers before they have been detected (Kingsley 2002, DFO 2007). Moreover, due to the extensive coastline and relatively low density of people in the area, some stranded beluga could be missed. It has also been suggested that young beluga are under-represented in such a database due to a lower buoyancy of their carcasses and their smaller size which reduces the probability of their detection (Caughley 1977, Béland et al. 1993, DFO 2007, Lesage et al. 2014). In the model, the number of dead newborns was therefore considered separately from that of older individuals (i.e. > 0 GLG; see section on priors).

PRIORS AND FITTING TO DATA

Priors for process parameters

We used 1913 as the start date for the model allowing for a long "adaptive period" and a 100 year total modelling period. Information on population size prior to the 1980s is highly uncertain. Hammill et al. (2007) incorporated harvest information into a surplus production model to back-calculate population size to 1866, assuming a maximum rate of increase r_{max}=1.04. Harvesting was extensive at that time, and the population was estimated to have decreased to approximately 4000 animals by 1913. To account for the large uncertainty, the initial population size was given a uniform prior ranging from 2000 to 10,000 individuals.

Estimates of mortality rates may be obtained from subsistence harvest data (Burns and Seaman 1985, Doidge 1990) or from beach-cast carcass records (Béland et al. 1988). In both cases, juveniles (small size, grey animals) are generally considered to be under-represented and mortality rates for these age classes are under-estimated (Burns and Seaman 1985, Béland et al. 1988, Doidge 1990, Lesage et al. 2014). Published estimates for newborn mortality suggest values ranging from 13.3% (Béland et al. 1992) to ~30% (smoothed values; Burns and Seaman 1985, Doidge 1990). To take into account this large range, the newborn mortality rate (M_{nb}, Fig. 1c) was given a prior following a Beta distribution with the first parameter (α) arbitrarily fixed to 2, and the second parameter set to follow a Gamma (6, 1) distribution. The resulting Beta distribution had a median of 23.9% with quartiles equal to 13.8% and 37.5%. Because the mortality can change each year, this distribution also allowed testing of the full range of mortality rates (0-100%).

Like newborns, yearlings are likely to have a higher mortality rates than adults (Burns and Seaman 1985, Béland *et al.*1988, Doidge 1990). However, they undergo lower mortality than neonates as they survived the high mortality associated with the peri-partum period and are in the process of weaning. Mortality rates of yearlings were estimated at 1.2 times adult mortality by Burns and Seaman (1985) and at 2.5 times adult mortality by Doidge (1990) assuming deposition of 2 and not 1 GLG. In the model, we assumed that mortality of yearlings (M_{1y}, Fig. 1c) was equal to twice that of adult mortality (M_{adult}).

Mortality rates of older beluga estimated by Burns and Seaman (1985, 7%), Doidge (1990; 8.4%) and Luque and Ferguson (2010, 3% to 8%) were obtained from hunted populations and thus include both natural and human-caused mortality. In our model, human-caused mortality was either included as catches (period 1912-1982) or absent (1983-2012). Even so, we assumed that the mortality rate applied to the "Immature" and "Mature" stages followed a Beta distribution where the first parameter was arbitrarily fixed to 2, and the second was sampled from a Gamma (30, 1) distribution. This resulted in a Beta distribution with a median at 5.4% and quartiles of 3.1 and 8.7%.

Not all available mature females reproduce each year. Five to 34% of the mature females can be non-pregnant and non-lactating individuals (Kleinenberg et al. 1964, Sergeant 1973, Burns and Seaman 1985, Doidge 1990). To account for this variability, pregnancy rate among available mature females (Pregnancy, Fig. 1c) was given the form of a Beta distribution with the first parameter (α) sampled from a Gamma (4,1) distribution and the second (β) sampled from a Gamma (20,15) distribution. This resulted in a Beta distribution with a median of 76.9% and quartiles of 58.9 and 98.7%. This parameterization allowed the model to test a large range of possible distributions across the entire range (0-100%) of pregnancy rates, including a quasi-uniform distribution when both parameters had values near 1.

Fitting of data and priors in observation parameters

The relationship between the true population size and its observed value was assumed to be:

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

with S_t the survey abundance estimates in year t, N_t the true population size and ε_{S_t} a multiplicative error term corresponding to the error around each aerial survey estimate (Gosselin et al. 2007). At the time when aerial surveys were conducted (end of August, early September), a portion of the annual mortality has taken place. Using the information from the carcass monitoring program, we determined that, as of September 1st, 83% of the newborn mortalities and 72% of the mortalities of older beluga had already occurred. These mortalities were thus applied in the model before fitting to observations.

The true proportion of young (newborns + yearlings) in the population and their proportion on survey photos were linked by:

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

with P_{S_t} the proportion of young estimated in the survey, P_{N_t} the true proportion of young in the population and $\varepsilon_{P_{S_t}}$ the error produced by a difference in detection rate between young and older beluga. No information was available to define this source of uncertainty and $\varepsilon_{P_{S_t}}$ was given a log-normal distribution with a zero location parameter and a precision ($\frac{1}{\sqrt{sd}}$) sampled from an arbitrary prior taking the form of a Gamma (20, 1) distribution. This resulted in a median CV of 23% around P_{S_t} with quartiles of 21% and 25%.

The number of dead beluga found each year through the carcass monitoring program was assumed to result from sampling in a binomial distribution with parameters corresponding to the number of beluga dead in that year, and the probability that these animals were found. Relationships for newborns and older individuals (i.e. excluding newborns) were described as:

For newborn $\qquad\qquad Strand_{nb_t} \sim Bin(pObs_{nb}, dead_{nb_t})$

For older individuals $\qquad Strand_{old_t} \sim Bin(pObs_{old}, dead_{old_t})$

with $\quad pObs_{nb} \sim$ Beta $(\alpha_{nb}, \beta_{nb}) \qquad$ and $\qquad pObs_{old} \sim$ Beta $(\alpha_{old}, \beta_{old})$

where $\alpha_{nb} \sim$ Uniform (0,1) $* \varphi_{nb} \quad$ and $\qquad \alpha_{old} \sim$ Uniform (0,1) $* \varphi_{old}$

$\qquad \beta_{nb} \sim (1 - \alpha_{nb}) * \varphi_{nb} \qquad\qquad \beta_{old} \sim (1 - \alpha_{old}) * \varphi_{old}$

There was no information to help define the values of $pObs_{nb}$ or $pObs_{old}$. Factors such as weather conditions (i.e. affecting human presence on shores), funding for the carcass monitoring program, could have influenced the effort and thus the probability of detection of beluga carcasses (DFO 2007). Therefore, $pObs_{nb}$ and $pObs_{old}$ were sampled from Beta

distributions with a mean value itself sampled from non-informative Uniform distributions bounded between 0 and 1. The error around the mean was controlled by a multiplying factor φ. Based on previous versions of the model that did not include an error term, we defined the value of φ_{nb} and φ_{old} as 100 and 300 respectively, assuming potential mean values for $pObs_{nb}$ and $pObs_{old}$ of 0.07 and 0.26. It resulted in quartiles of 0.052, 0.086 for $pObs_{nb}$, and 0.242, 0.277 for $pObs_{old}$.

Parameter estimation, model diagnostics and sensitivity tests

We obtained posterior estimates of all the parameters using a Gibbs sampler algorithm implemented in JAGS (Plummer 2003). Results were examined in the R programming language (R core team 2013), using packages R2jags and coda.

In addition to visual examination through trace plots, convergence between MCMC chains was tested using the Gelman-Rubin diagnostic (Gelman and Rubin 1992, Brooks and Roberts 1998) for seven variables of interest describing the process (M1, M3, Preg) and the observation (α_{nb} and α_{old} for carcasses detection, Npop$_{1988}$ as the abundance estimate at the first year of aerial survey, Npop$_{2012}$ as the last abundance estimate). The stationarity of each chain was checked using the Geweke statistic (Geweke 1992). Cross-correlation among the selected variables was tested.

After several tests, the final run included 3 chains of 1,500,000 iterations in which we kept one sample every 500 iterations after a burn-in phase of 500,000 iterations. This resulted in a final set of 6000 samples (2000 samples per chain).

Sensitivity of the results to the initial population structure was tested using two alternative age structures. The first was obtained from a Leslie matrix (Leslie 1945) using population parameters based the carcass monitoring data (following the methodology described in Caughley 1977 and Béland et al. 1988). The second test assumed that all age classes comprised the same proportion of the population.

Sensitivity of the results to the prior distributions of parameters M$_{nb}$, M$_{adult}$, Preg, pObs$_{nb}$, and pObs$_{old}$ was tested by changing the value of one parameter while keeping the others fixed.

Sensitivity of the results to the datasets used to fit the model was also tested. First, the model was fitted only to abundance estimates obtained from the aerial surveys. Then, information on the proportion of young, on the number of newborn and older individuals found dead were successively added in new runs. In those runs, model priors were the same as in the main model.

We also tested the effect of removing the 2009 abundance estimate from the fitting process to evaluate the weight of this particularly low value in the model results.

All sensitivity tests were conducted using 3 chains of 1,000,000 iterations with one sample taken every 100 iterations and a burn-in phase of 500,000 iterations. This lower number of iterations was considered sufficient to test for major deviations from the main model.

RESULTS

MODEL DIAGNOSTICS

The Gelman-Rubin diagnostic confirmed the convergence between the three chains for each variable of interest, with R-hat diminishing to values below 1.1 (Fig. 2). Trace plots showed good mixing for each chain, and a stationary distribution (Fig. 3, Geweke's diagnostic, all Z-scores < 1.96).

PARAMETER ESTIMATION

Posterior distributions of newborn mortality (M1), adult mortality (M3) and pregnancy (Preg) used in the "adaptative" part of the model (1912-1982) are presented in Fig. 3. Median of M1 was 23.7% (95% CI 16.5 - 32.7). M3 had a median of 6.1% (95% CI 5.0 - 7.2) and the pregnancy rate of mature females available for reproduction (Preg) was 76% (95% CI 64.5 - 85). The corresponding "population wide" pregnancy rate was estimated at 32.6% (95% CI 27.6 - 36.9). These values correspond to the medians of the year-specific values estimated in the "fitting part" of the model (1983-2012, see Material and Methods).

The cross-correlation tests (Table 2) showed that the model tended to decrease the probability of detection of carcasses of newborns or older individuals (i.e. excluding newborns) when it increased the newborn mortality or the adult mortality, respectively. The probability of detection of older beluga carcasses was negatively correlated with the 1988 population size estimate. Interestingly, a decrease in the 2012 population size estimate was strongly correlated with an increase in adult mortality but not with newborn mortality.

Newborn mortality (M_{nb}), adult mortality (M_{old}), pregnancy rates (Pregnancy), and the probability of detecting carcasses of dead newborn ($pObs_{nb}$) and older beluga ($pObs_{old}$) were estimated for each year of the "fitting part" (1983-2012). From 1983 to 1997, annual newborn mortality was relatively stable with median values varying from 14 to 27% with peaks every 3 to 4 years (Fig. 4a). In contrast, the period 1998-2012 was highly unstable with median values for annual newborn mortality ranging from 8 to 69% and higher peaks appearing every two years starting in 2008.

Posterior distributions for annual adult mortality showed an important update of the prior distribution with a reduced variability around the median value (Fig. 4b). The median of the annual adult mortality was 6.1% but ranged from 4% (1987, 2005) to 7.8% (1989, 1993), even reaching 8.7% in 2004. Overall, adult mortality rates were less variable across the period 1984-2012 than those of newborns.

Like newborn mortality, annual pregnancy rates were relatively stable at around 80% between 1983 and 1998, becoming unstable afterwards (Fig. 4c). Changes in pregnancy rates were more evident when examining "population wide" pregnancy rate (Fig. 4d). Small peaks in pregnancy occurred every 3 years until the mid-1990's. Two higher peaks occurred afterwards in 2000 and 2003, with more than 50% of the females being pregnant, separated by two years of low pregnancy rates (around 14.5%). Another period of high pregnancy rates occurred in 2006 and 2007, followed by a succession of low and high pregnancy rates starting in 2008.

Posterior distributions of the probability of detecting carcasses of newborns showed an important update from the prior distribution ($pObs_{nb}$, Fig. 4e). Before 2007, the median value of $pObs_{nb}$ was generally stable around 5.6% (95%CI 2.1-11.6%) after which it increased with peaks in 2008 (7.9%; 95%CI 3.9-14.2%) and 2012 (11.1%; 95%CI 6.6-17.7%). The probability of detecting of carcasses of older individuals (i.e. 1 year old and older) was updated each year from its prior. However, there was no change in this probability during the period 1983-2012 (Fig. 4f) with a median value of 20.2% (95%CI 14.5-27.2%).

POPULATION TRAJECTORY AND POPULATION STRUCTURE

The model estimated the SLE beluga population at 1017 individuals (95%CI 866-1200; Fig. 5) in 1988. The population remained stable or showed a slight increase until the early 2000s (growth rate ~ 0.13% by year between 1983 and 2002). Thereafter, the estimated population decreased to 889 individuals (95%CI 672-1167) in 2012 (growth rate − 1.13% by year). The model estimate for 2009 (934 with 95%CI 760-1150) was notably higher than the value obtained from

the aerial photographic survey flown in the same year (676 beluga with 95%CI 470-882; Gosselin et al. 2014).

Consistent with the pattern observed in the pregnancy rates (Fig. 4d), the proportion of young in the population showed small peaks every 3 years until the mid-90's, then remained at around 13.7% until 1998 (Fig. 6). Thereafter, the proportion of young beluga (0-1 years old) decreased to 8.9% in 2000 then showed two high peaks in 2001 and 2005 (17.7% and 18.3% respectively) separated by a low value in 2003 (4.3%). After 2005, the proportion of young remained lower than before 1998 with median values around 10.3%. The output of the model fitted reasonably well to the proportion of young estimated from the aerial photographic surveys. The fit, however, was better for the period after 1997.

The number of newborn deaths predicted by the model followed very closely the patterns observed in the carcass data (Fig. 7). Two periods were apparent. Between 1983 and 2007, the model estimated that the median number of newborn beluga dying each year varied around 22 individuals (range of medians: 11 - 38 individuals). Then, for 2008, 2010 and 2012, the model estimated respectively 75, 99 and 97 newborn deaths. Those high values were associated with a higher pregnancy rate in the previous year and a higher newborn mortality. Moreover, the model suggested that the large number of newborn carcasses found in 2012 was in part explained by a higher number of deaths, but also attributed to an increase in the probability of detection (Fig. 4e)

Model estimates of the number of deaths among beluga aged 1-year and older were consistent with observations from the carcass monitoring program (Fig. 8). Results did not indicate a trend in the number of deaths but showed, however, large variability. The model estimated that between 1983 and 2012, the median number of beluga aged 1-year and older dying annually was around 65 individuals, ranging from 45 to 90 beluga (median range).

The evolution of the proportion of the population in each age class (Fig. 9) highlights the consequences of the important changes in productivity and newborn mortality that occurred between 1999 and 2006 (Fig. 4a, c and d), and their propagation through the age structure. The model estimated that the proportion of immature individuals in the population has declined since 1999, with a corresponding increase in the proportion of mature beluga. However, this increase did not result in an increase of the number of mature individuals (Fig. 9). Visualising the population structure as an age pyramid (Fig. 10) reveals a gap created in 2002 and 2003 between the two peaks of production in 2001 and 2004, and its propagation through the population. The model also estimated a decrease in the proportion of newborns in the population from 6-8% before 1999 to 4-6% after 2007.

SENSITIVITY TO PRIORS

The choice of the initial population structure did not affect model parameter estimates (Fig. 11, Appendix 1), demonstrating the usefulness of the "adaptive part" of the model and the robustness of the final age structure.

The newborn mortality estimated by the model was highly sensitive to the choice of its prior distribution. The use of a non-informative flat prior (beta (1,1), equivalent to a uniform(0,1) distribution), showed that newborn mortality was not updated for several years (Fig. 12). The model compensated higher newborn mortality by increasing the pregnancy rate and reducing the probability of detecting newborn carcasses. It did the opposite when newborn mortality decreased. This compensation resulted in a limited effect on the 1988 population size estimate, but a larger one on the 2012 population size estimate, which was inversely correlated to the prior value for newborn mortality.

The model was also highly sensitive to the prior for adult mortality. Extreme values (median 15.2%) were updated (decreased to 7.6%) but the model using this prior gave the lowest estimate for the 2012 population size (median = 600 beluga) with a population declining since 1913 (figure not shown). Conversely, priors with a lower median value than the one used in the main model resulted in continual growth from the end of the 1950's to the present without a large effect of the low population estimate obtained from the 2009 aerial survey (i.e. poor fit to survey estimates).

Pregnancy rate posteriors were highly sensitive to their prior distribution, but the effect on the population size estimates for 1988 and 2012 was limited, even for the two extreme cases tested (median 1988 = 1015-1024 and median 2012 = 854-898, compared to 1017 and 889 for the main model). Changes in pregnancy rate were compensated for the most part by a decrease in adult mortality.

Modifications of the value of φ_{nb} and φ_{old}, respectively controlling the variance around pObs$_{nb}$ and pObs$_{old}$, had only a small effect on the results. Reducing the variability (φ_{nb} = 300 and φ_{old} = 900) decreased the value of newborn mortality estimated by the model and slightly increased the population size estimated for 2012. Increasing the variability (φ_{nb} = 30 and φ_{old} = 100) had the opposite effect.

SENSITIVITY TO THE DATASETS

The model fitted exclusively to aerial survey abundance estimates (Test Dataset Sensitivity 1, TDS1) estimated a slightly higher 1988 population size than the main model and a lower population size in 2012 (776 vs 889 for the main model). This difference was associated with an overall increase in newborn mortality and a higher variability of the newborn and adult mortalities (Fig. 11, Appendix 1, and Appendix 2 Fig.1).

When using both survey abundance estimates and the information on the proportion of young detected on aerial photos (TDS2), results were similar to TDS1, with only a small decrease in pregnancy rate and in variability around newborn mortality (Appendix 1). Population estimates for the period 1983-2012 (Appendix 2 Fig. 2) varied more widely between years but the general population trajectory was similar to TDS1.

Incorporating the newborn carcass dataset (TDS3) decreased newborn mortality estimate to a value close to that of the main model, and greatly affected adult mortality estimates (TDS3 median = 0.55 vs 0.62 and 0.61 for TDS2 and the main model respectively). This affected population size estimates by lowering the 1988 value by more than 50 individuals and increasing the 2012 estimate close to that of the main model (874 vs 889; Appendix 2 Fig.3).

Integrating the carcass data for older beluga (i.e. excluding carcass data for newborns) in the fitting process resulted in a higher mortality rate for adults with a reduced variability (Fig. 11). This leaded to a continuous decline since 1913, with a 1988 estimate higher than in TDS3 and in the main model, but a lower 2012 estimate (Appendix 2 Fig. 4).

The inclusion of the entire carcass dataset (i.e. the main model) resulted in a slower decline in abundance in recent years, and thus a poorer fit to the 2009 aerial survey abundance estimate, than when using only aerial surveys. However, the carcass data may have a disproportionate weight in the model because, unlike surveys, they are available every year. This could be problematic because photographic aerial surveys were recommended as the most reliable index of population size (St. Lawrence Beluga Recovery Team 1995). Testing the sensitivity of the model using several subsets of the carcass data, in order to reduce its relative weight in the model, revealed large differences in the 1988 and 2012 population size estimates, depending on the years sampled and sampling frequency.

Removing the 2009 abundance estimate from the fitting process changed the estimated population trajectory, with the population increasing since the 1950s then stabilizing around 1200 beluga over the last 6-8 years (Appendix 2 Fig. 8). The initial increase was linked to a lower estimated adult mortality than in the main model. As per the main model, the change in population trajectory in later years corresponded to changes in age structure and population dynamic parameters starting around 1999.

DISCUSSION

POPULATION TRAJECTORY AND STRUCTURE

Previous work on population trends has focused on survey estimates. The present model combined information from different data sources into a single framework to yield a plausible population trajectory that followed the constraints of the age structure and life-history parameters of SLE beluga.

The model estimates that the SLE beluga population had been stable or increasing at a slow rate since the end of the hunt in the 1960s up until the late 1990s, with around 1000 individuals in 1998. This result is in agreement with previous trend analyses (Hammill et al. 2007). But, the model then suggests that a steady decline in abundance started around 2000. The rate of this decline depended on which dataset was fitted (the steepest decline was obtained when fitting only to aerial survey data), but all versions of the model agreed that numbers have been decreasing in recent years.

The model also revealed internal changes in population dynamics and age-structure that have occurred along with this decline. Indeed, estimates of the population parameters that were allowed to vary across years helped distinguish two periods that corresponded to those shown by the population trajectory. The period 1984-1998 was characterized by relatively stable newborn mortality (median values from 14% to 27% with peaks every 3 to 4 years, Fig. 4a) and stable pregnancy rates (around 30%, with small peaks every 3 years, Fig. 4d). During this period, population age structure was stable with the ratio of mature:immature beluga close to 58:42%, and the proportion of newborns around 7.5%.

In contrast, the period 1999-2012 was characterized by demographic instability and severe changes in population parameters and age structure. The year 1999 stood out by its unusually high newborn mortality (~40%). The following year, pregnancy rates were particularly high (>50%), presumably because the 1999 mortalities led to more females being available for reproduction. From then on, the period was marked by peaks of high newborn mortality (2002-2003, 2008, 2010, 2012) interspersed by peaks of high pregnancy rates (2003, 2009, 2011), themselves separated by periods of lower-than-average fecundity (e.g., ~15% in 2001-2002).

A particularly striking pattern emerged over the last 6 years with female reproduction apparently changing from a 3-year cycle (with a third of mature females pregnant each year) to a 2-year cycle (with about half of the females pregnant). This phenomenon was accompanied by an overall increasing trend in newborn mortality (i.e., both peaks and troughs being higher). The effects of these changes on the population age structure are obvious in Figs. 9 and 10. The proportion of newborns deviated from its 3-year cycle and started to oscillate strongly in the early 2000s, while showing a decreasing trend. At the same time, the proportion of mature beluga began to increase (but their absolute numbers stayed constant), resulting in a ratio of mature:immature of 66:33% by 2012.

UNCERTAINTY AND SENSITIVITY

The strength of this model was its ability to incorporate data from multiple sources, thus providing more information for inference. Because each of these data sources was characterized by large uncertainty, we used a Bayesian framework to separate errors associated with observation from natural variability in population dynamics, and to introduce expert knowledge in the form of prior distributions. Sensitivity tests revealed, however, that results were sensitive to some of the priors and therefore must be interpreted with caution. For instance, the 2012 population size was particularly sensitive to the choice of priors for adult and newborn mortality. Additional information on key life-history parameters specific to this population would assist in prior formulation and would likely result in better posterior updates.

The results were also sensitive to the datasets used to fit the model. With no other information than the abundance estimates, the model blamed the decline in abundance on high overall adult mortality. Adding the proportion of young (newborns and yearlings) informed the model about changes in population structure, but it could not explain recent mortality events. The stranding data were essential for the model to find a mechanism for the decline in abundance. However, they also made it harder for the model to fit the 2009 abundance estimate. Excluding newborns, the number of beluga carcasses found remained fairly stable from 1984 to 2012, which could be interpreted as evidence that population abundance did not vary much across that period, in contradiction to results from the latest survey. The model explained this in part by suggesting that adults were becoming proportionally more numerous than immature beluga, thus keeping their numbers in beluga carcasses relatively constant. Nonetheless, carcass data may have a disproportionate weight because of their higher frequency (annual) than surveys (multi-year), which has an effect on estimates of the rate of decline of the population. However, sensitivity tests also showed the important effect of the 2009 abundance estimate on the model predictions, demonstrating the large influence of the data provided by the photographic surveys in the fitting process. Interestingly, even the model without the 2009 survey identified the same changes in age structure and population parameters than the main model.

Despite this sensitivity, several points increase our confidence in the model's main results. Numerous parameters were strongly updated from their prior distributions, and their estimated values fit with previous studies. The pregnancy rate, in particular, was estimated at 32.6% during the period 1984-1998, in complete agreement with the 3-year calving interval that is usually assumed for the species (Sergeant and Brodie 1975). Moreover, small regular peaks in fecundity suggest some degree of synchrony among females in part of the population. Such synchrony had already been suggested by Kingsley and Hammill (1991) as an explanation for the change in the proportion of young observed between the 1988 and 1990 aerial surveys. Interestingly, in the model, the proportion of young (newborns and yearlings) estimated for this period did suggest a low value in 1988 and a high value in 1990 (although the 1988 proportion of young was not used in the model because of concerns with the methodology of the survey).

A long-term photo-identification program of live SLE beluga (1989-2012) indicated changes in age structure and calf production similar to those suggested by the model (Michaud 2014). In particular, years of high pregnancy rates predicted by the model for the period 2004-2012 were followed by observations of high calf production in the field, supporting the conclusion that pregnancy rates changed from a stable to a highly variable pattern in the early 2000's.

Finally, aerial visual surveys of the SLE beluga population were also conducted between 2001 and 2009 (Gosselin et al. 2014) and the trend in the abundance estimates obtained from this source follow closely the prediction of the model (Fig. 13)

INSIGHTS INTO MECHANISMS OF POPULATION DECLINE

The model strongly suggests that the SLE beluga population has not been increasing significantly since being afforded protection, and has recently begun to decrease. Moreover, the model raises concerns that the population has experienced severe changes in age structure. The reason for the lack of recovery previous to 1998 remains unknown, but the model does provide insights into the proximal mechanisms responsible for the recent decline.

In 1999, 2002 and 2003, the population appears to have experienced events of high newborn mortality. Initially, these mortality events were not reflected in survey estimates, likely because, as is observed in other long-lived species, the structure of the beluga population prevented short-term variations in abundance in response to punctual changes in life-history parameters. The model suggests, however, that these events had a cascading effect on the reproductive pattern of females. Females having lost their young became available for reproduction earlier than the normal 3-year cycle, resulting in years with over half of the mature females being pregnant at the same time. These peaks were usually followed by peaks of high newborn mortality, suggesting that the population could not support these excessive birth rates. This would in turn free more females for reproduction the next year. The decrease in numbers observed in recent surveys (Gosselin et al. 2014) appears to be a lagged response resulting from lower recruitment propagating through the population.

Although the events that initially triggered this perturbation are not known, the problem seems to have worsened in the last six years, following a harmful algal bloom due to *Alexandrium tamarense* producing a highly toxic saxitoxin which caused high mortality in 2008 (Truchon et al. 2013). This event seems to have extended the period of low recruitment and resulted in a highly synchronized 2-year reproductive cycle that is characterized by rising newborn mortality. Toxic algal blooms also occurred in 1996 and 1998 without apparent effects on mortality. .The role of chronic sub-lethal exposure to saxitoxins on beluga reproduction and health is not known (Scarratt et al. 2014).

The fact that years of high birth rates appear to correspond to years of high newborn mortality also suggests that resources may be limiting. This is intriguing because the SLE beluga population is believed to be far below its historical carrying capacity. We note that the change between the stable and unstable periods also corresponds to major changes in the environment, including a shift in physical conditions (e.g. increase in water temperature, decrease in ice coverage) and a decrease in spring spawning herring biomass (Plourde et al., 2014), potentially an important prey of beluga. As a k-selected species, beluga should be well adapted to coping with environmental variability. There are, however, other examples of large marine mammal population that have reacted quickly and negatively to changes in prey availability (e.g., Northern right whales in response to low copepod abundance; Pacific killer whales in response to declines in salmon abundance; Greene and Pershing 2004, Ford et al. 2009).

Moreover, median adult mortality was estimated by the model at 6.1%. Although this value falls in the 3% to 8% range estimated by Luque and Ferguson (2010) for five beluga populations living in northern Canada, those are hunted populations. One would expect a lower value for SLE beluga which has been protected from hunting since 1979. The lack of recovery, high overall adult mortality and highly variable newborn survival could all be signs that the population is in fact limited by resources in its environment, particularly subject to climate variability and cascading effects (Plourde et al. 2014). This underlines the importance of maintaining a critical population to withstand periodic downturns, in particular by addressing anthropological factors that could delay recovery.

REFERENCES CITED

Anonymous. 1979. Beluga protection regulation amendment P. C. 1979-367, 15 February 1979. Registration SOW79-169 *Fisheries Act.* Canada Gazette, part 2, vol. 113, no 4,28/II/79: 738.

Béland, P., Vézina, A. and Martineau D. 1988. Potential for growth of the St. Lawrence (Québec, Canada) beluga whale (*Delphinapterus leucas*) population based on modelling. J. Cons. Int. Explor. Mer 45: 22-32.

Béland, P., De Guise, S. and Plante R. 1992. Toxicologie et pathologie des mammifères marins du Saint-Laurent. Institut National d'Écotoxicologie du Saint Laurent. Toronto : World Wildlife Fund – Canada. 99 p.

Béland, P., De Guise, S., Girard, C., Lagacé, A., Martineau, D., Michaud, R., Muir, D.C.G., Norstrom, R.J., Pelletier, E., Ray, S. and Shugart, L.R. 1993. Toxic compounds and health and reproductive effects in St Lawrence beluga whales. J. Gt. Lakes Res. 19: 766-775.

Brodie, P.F. 1971. A reconsideration of aspects of growth, reproduction, and behavior of the white whale (*Delphinapterus leucas*), with reference to the Cumberland Sound, Baffin Island, population. J. Fish. Res. Board Can. 28: 1309-1318.

Brooks, S. P. and Roberts, G. O. 1998. Assessing Convergence of Markov Chain Monte Carlo Algorithms. Stat. Comput. 8: 319–335.

Burns, J.J., and Seaman G.A. 1985. Investigations of beluga whales in coastal waters of western and northern Alaska: II. Biology and ecology. Final rep. Prepared for U.S.Dep. Commer., NOAA, Natl. Ocean Serv., Anchorage, AK, contract NA81RAC00049. Alaska Dep. Fish and Game, Fairbanks. 129 p.

Caughley, G. 1977. Analysis of vertebrate populations. Wiley, New York. 234 pp.

Cook, F.R. and Muir, D. 1984. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC): history and progress. Can. Field-Nat. 98: 63–70

COSEWIC 2004. COSEWIC assessment and update status report on the beluga whale *Delphinapterus leucas* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. ix + 70 pp.

De Valpine, P., and Hastings A. 2002. Fitting population models incorporating process noise and observation error. Ecological Monographs 72: 57-76.

DFO. 2007. Proceedings of the workshop on the St. Lawrence Estuary beluga – review of carcass program; November 14 - 17, 2005. DFO Can. Sci. Advis. Sec. Proceed. Ser. 2007/005. Viii + 88 p.

Doidge, D.W. 1990. Age and stage based analysis of the population dynamics of beluga whales, *Delphinapterus leucas*, with particular reference to the northern Quebec population. Thesis (Ph.D.). MacDonald College. McGill university, Montréal, Qc. 190 p.

Doniol-Valcroze, T., Hammill, M.O., and Lesage, V. 2011. Information on abundance and harvest of eastern Hudson Bay beluga (*Delphinapterus leucas*). DFO Can. Sci. Advis. Sec. Res. Doc. 2010/121. iv + 13 p.

Ford, J.K.B, Ellis, G.M., Olesiuk, P.F., and Balcomb, K.C. 2009. Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator?.Biology Letters doi: 10.1098/rsbl.2009.0468

Gelman, A. and Rubin, D.B. 1992. Inference from iterative simulation using multiple sequences, Stat. Sci. 7: 457-511.

Gelman A. and Shirley K. 2011. "Inference from simulations and monitoring convergence." In Handbook of Markov chain Monte Carlo (ed S. Brooks, A. Gelman, G. Jones, X.L. Meng), Chapman & Hall, pp. 163-174.

Geweke, J. 1992. Evaluating the accuracy of sampling-based approaches to calculating posterior moments. In Bayesian Statistics 4 (ed J.M. Bernado, J.O. Berger, A.P. Dawid and A.F.M. Smith). Clarendon Press, Oxford, UK. pp. 1-31

Gosselin, J-F., Lesage V. and Robillard A. 2001. Population index estimate for the beluga of the St. Lawrence River Estuary in 2000. DFO Can. Sci. Advis. Sec. Res. Doc. 2001/049, 21 p.

Gosselin, J-F., Hammill, M.O., and Lesage V. 2007. Comparison of photographic and visual abundance indices of belugas in the St Lawrence Estuary in 2003 and 2005. DFO Can. Sci. Advis. Sec. Res. Doc.2007/025. 28p.

Gosselin, J-F., Hammill, M.O. and Mosnier A. 2014. Summer abundance indices of St Lawrence estuary beluga (*Delphinaterus leucas*) from a photographic survey in 2009 and 28 line transect surveys from 2001 to 2009. DFO Can. Sci. Advis. Sec. Res. Doc. 2014/021. iv + 52 p.

Greene, C.H. and Pershing A.J. 2004. Climate and the conservation biology of North Atlantic right whales: the right whale at the wrong time? Front. Ecol. Environ. 2: 29–34

Hammill, M.O., Measures L.N., Gosselin J.-F. and Lesage V. 2007. Lack of recovery in St. Lawrence Estuary beluga. DFO Can. Sci. Advis. Sec., Res. Doc. 2007/026, 23 p.

Kingsley, M.C.S. 1993. Census, trend, and status of the St Lawrence beluga population, 1992. Can. Tech. Rep. Fish. Aquat. Sci. 1938 : vi + 17 p. + Appendices.

Kingsley, M.C.S. 1996. Population index estimate for the belugas of the St. Lawrence in 1995. Can. Tech. Rep. Fish. Aquat. Sci. 2 117. 38 pp. + Appendices.

Kingsley, M.C.S. 2002. Status of the belugas of the St Lawrence estuary, Canada. NAMMCO Scientific Publications 4: 239-257.

Kingsley, M.C.S. and Hammill, M.O. 1991. Photographic census surveys of the St Lawrence beluga population, 1988 and 1990. Can. Tech. Rep. Fish. Aquat. Sci. 1776. 19 pp.

Kleinenberg, S.E., Yablokov, A.V., Bel'kovich, B.M., and Tarasevich. M.N. 1964. Beluga (*Delphinapterus leucas*): investigation of the species. Akad. Nauk SSSR, Moscow. Translated from Russian. Israel Program for Sci. Transl., Jerusalem, 1969. 376 p.

Klevezal, G.A. 1996. Recording structures of mammals: determination of age and reconstruction of life history. – Rotterdam/Brookfield, A.A. Balkema. 274 pp.

Lesage, V. and Kingsley, M.C.S. 1998. Updated status of the St Lawrence River population of the Beluga, *Delphinapterus leucas*. Can. Field-Nat. 112: 98-113

Lesage, V., Measures, L., Mosnier, A., Lair, S., Michaud, R. and Béland, P. 2014. Mortality patterns in St. Lawrence Estuary beluga (*Delphinapterus leucas*), inferred from the carcass recovery data, 1983-2012. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/118. iv + 23 p

Leslie, P.H. 1945. "The use of matrices in certain population mathematics". Biometrika, 33: 183–212.

Luque, S.P., Higdon, J.W., and Ferguson, S.H. 2007. Dentine deposition rates in beluga (*Delphinapterus leucas*): an analysis of the evidence. Aquat. Mamm. 33: 241-245.

Luque, S.P. and Ferguson, S.H. 2010. Age structure, growth, mortality, and density of belugas (*Delphinapterus leucas*) in the Canadian Arctic: responses to environment?, Polar Biol. 33: 163-178.

Michaud, R. 2014. St. Lawrence Estuary beluga (*Delphinapterus leucas*) population parameters based photo-identification surveys, 1989-2012. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/130. iv + 27 p.

Mosnier, A., Lesage, V., Gosselin, J.-F., Lemieux Lefebvre, S., Hammill, M. O., and Doniol-Valcroze, T. 2010. Information relevant to the documentation of habitat use by St. Lawrence beluga (*Delphinapterus leucas*), and quantification of habitat quality. DFO Can. Sci. Advis. Sec., Res. Doc. 2009/098. iv + 35 p.

Plourde, S., Galbraith, P., Lesage, V., Grégoire, F., Bourdages, H., Gosselin, J.-F., McQuinn, I., and Scarratt, M. 2014. Ecosystem perspective on changes and anomalies in the Gulf of St. Lawrence: a context in support of the management of the St. Lawrence beluga whale population. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/129. v + 29 p.

Plummer M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling; Proceedings of the 3rd International Workshop on Distributed Statistical Computing; Vienna, Austria. 10 p.

R Core Team 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 3551 p.

Reeves, R. R. and Mitchell E. 1984. Catch history and initial population of white whales (*Delphinapterus leucas*) in the River and Gulf of St. Lawrence, Eastern Canada. Nat. Can. 111: 63-121.

Robeck, T.R., Monfort, S.L., Calle, P.P., Dunn, J.L., Jensen, E., Boehm, J.R., Young, S., and Clark, S.T. 2005. Reproduction, growth and development in captive beluga (*Delphinapterus leucas*). Zoo Biology 24: 29-49.

St. Lawrence Beluga Recovery Team. 1995. St. Lawrence beluga recovery plan. Fisheries and Oceans Canada and World Wildlife Fund (Canada), Toronto, Ont. 73 p.

Sergeant, D.E. 1973. Biology of white whales (*Delphinapterus leucas*) in Western Hudson Bay. J. Fish. Res. Board Can. 30: 1065-1090.

Sergeant, D.E. and Brodie P.F. 1975. Identity, abundance and present status of white whales (*Delphinapterus leucas*) in North America. J. Fish. Res. Board Can. 32: 1047-1054.

Scarratt, M., Michaud, S., Measures, L., Starr, M. 2014. Phycotoxin analyses in St. Lawrence Estuary beluga. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/124. v + 16 p.

Stenson, G.B., Hammill, M.O., Gosselin, J.-F., and Sjare, B. 2000. 1999 pup production of harp seals, *Phoca groenlandica*, in the Northwest Atlantic. DFO Can. Stock Assess. Res. Doc. 2000/080. 35 p.

Stewart R.E.A., Campana S.E., Jones C.M., and Stewart B.E. 2006. Bomb radiocarbon dating calibrates beluga (*Delphinapterus leucas*) age estimates. Can. J. Zool. 84: 1840-1852.

Suydam, R.S. 2010. Age, growth, reproduction and movements of beluga whales (*Delphinapterus leucas*) from the eastern Chukchi Sea. Ph.D. thesis. University of Washington. 152 p.

Truchon, M.-H., Measures, L.N. L'Hérault, V, Brêthes, J-C., Galbraith, P., Harvey, M., Lessard, S., Starr, M. and Lecomte N. 2013. Marine Mammal Strandings and Environmental Changes: A 15-Year Study in the St. Lawrence Ecosystem. PLoS ONE 8: e59311. doi:10.1371/journal.pone.0059311

Vladykov, V.D. 1944. Etude sur les mammifères aquatiques. III. Chasse, biologie, et valeur économique du marsouin blanc ou béluga (*Delphinapterus leucas*) du fleuve et du golfe Saint-Laurent. Québec. Département. des Pêcheries. 194 p.

Table 1. Description of the variables used in the figures and tables. For more details, see the Material and Methods section.

M_{nb}	Newborn Mortality
M1	Median value of M_{nb} for the period 1983-2012
M_{adult}	Adult Mortality
M3	Median value of M_{adult} for the period 1983-2012
Pregnancy	Pregnancy rate
Preg	Median value of "Pregnancy" for the period 1983-2012
$pObs_{nb}$	Probability of detecting newborn beluga carcasses
α_{nb}	Mean of $pObs_{nb}$ in each year during the period 1983-2012
φ_{nb}	Value of the multiplying factor controlling the variance around α_{nb}
$pObs_{old}$	Probabiilty of detecting carcassesof beluga 1 year-old and older
α_{old}	Mean of $pObs_{old}$ in each year during the period 1983-2012
φ_{old}	Value of the multiplying factor controlling the variance around α_{old}
Npop1988	Population size estimated by the model for 1988
Npop2012	Population size estimated by the model for 2012

Table 2. Cross-correlation matrix among posterior distributions of eight selected model variables (M1, M3, Preg, PregPop, α_{nb}, α_{old}, Npop1988, and Npop2012).See Table 1 for a description of variables.

	M1	M3	Preg	PregPop	α_{nb}	α_{old}	Npop1998	Npop2012
M1	1,00							
M3	-0,08	1,00						
Preg	0,01	0,07	1,00					
PregPop	0,07	-0,01	0,38	1,00				
α_{nb}	-0,42	< 0,01	-0,11	-0,11	1,00			
α_{old}	0,09	-0,63	-0,07	< 0,01	0,15	1,00		
Npop1998	0,02	0,44	< 0,01	< 0,01	-0,26	-0,76	1,00	
Npop2012	-0,04	-0,70	0,03	0,03	-0,04	0,29	-0,07	1,00
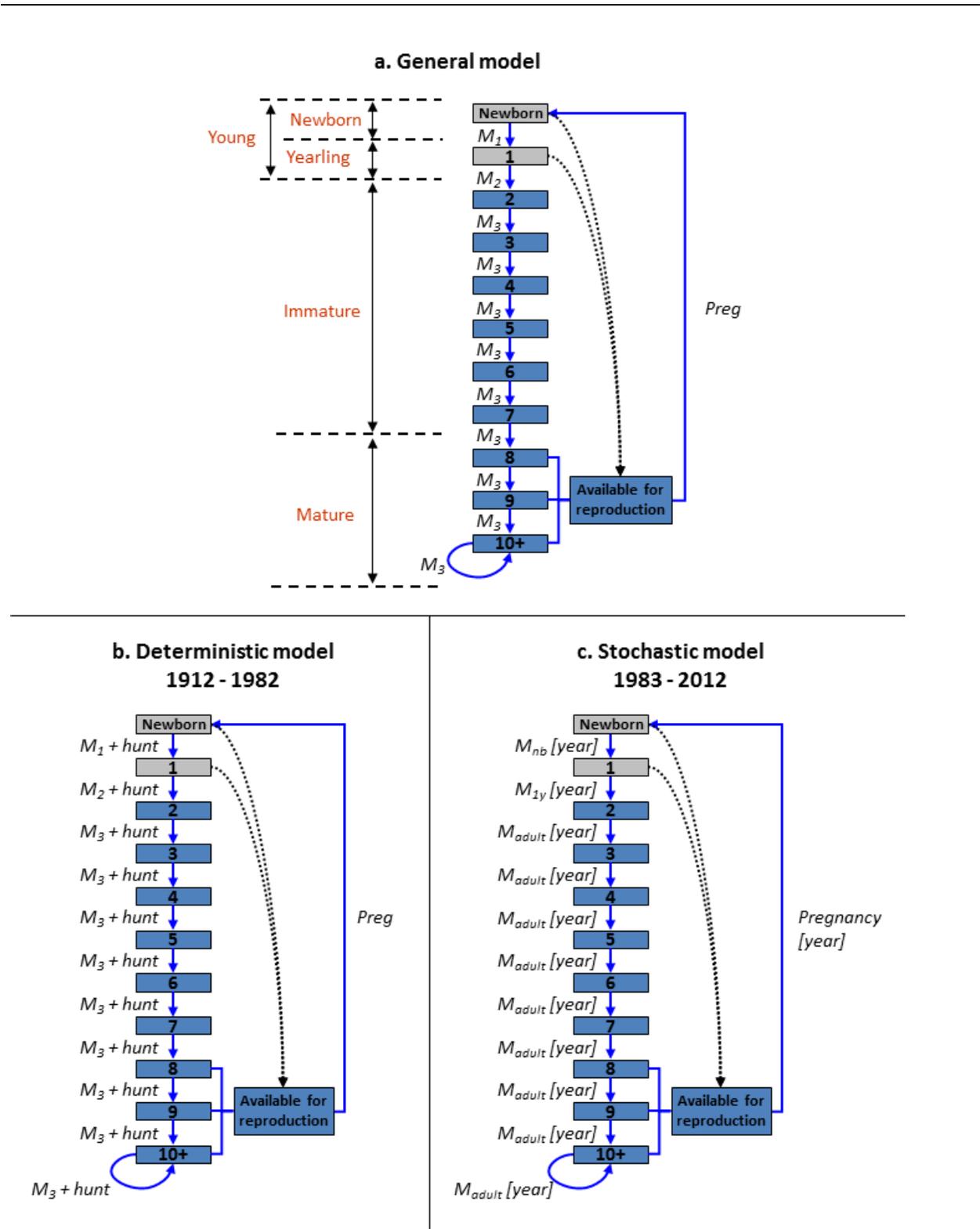
Figure 1. Graphical representation of a) the general form of the population dynamics part of the model b) the deterministic form of the population dynamics model applied between for the 1913-1982 period including fixed parameters and hunting removals, c) the stochastic form of the model estimating parameters each year between 1983 and 2012.
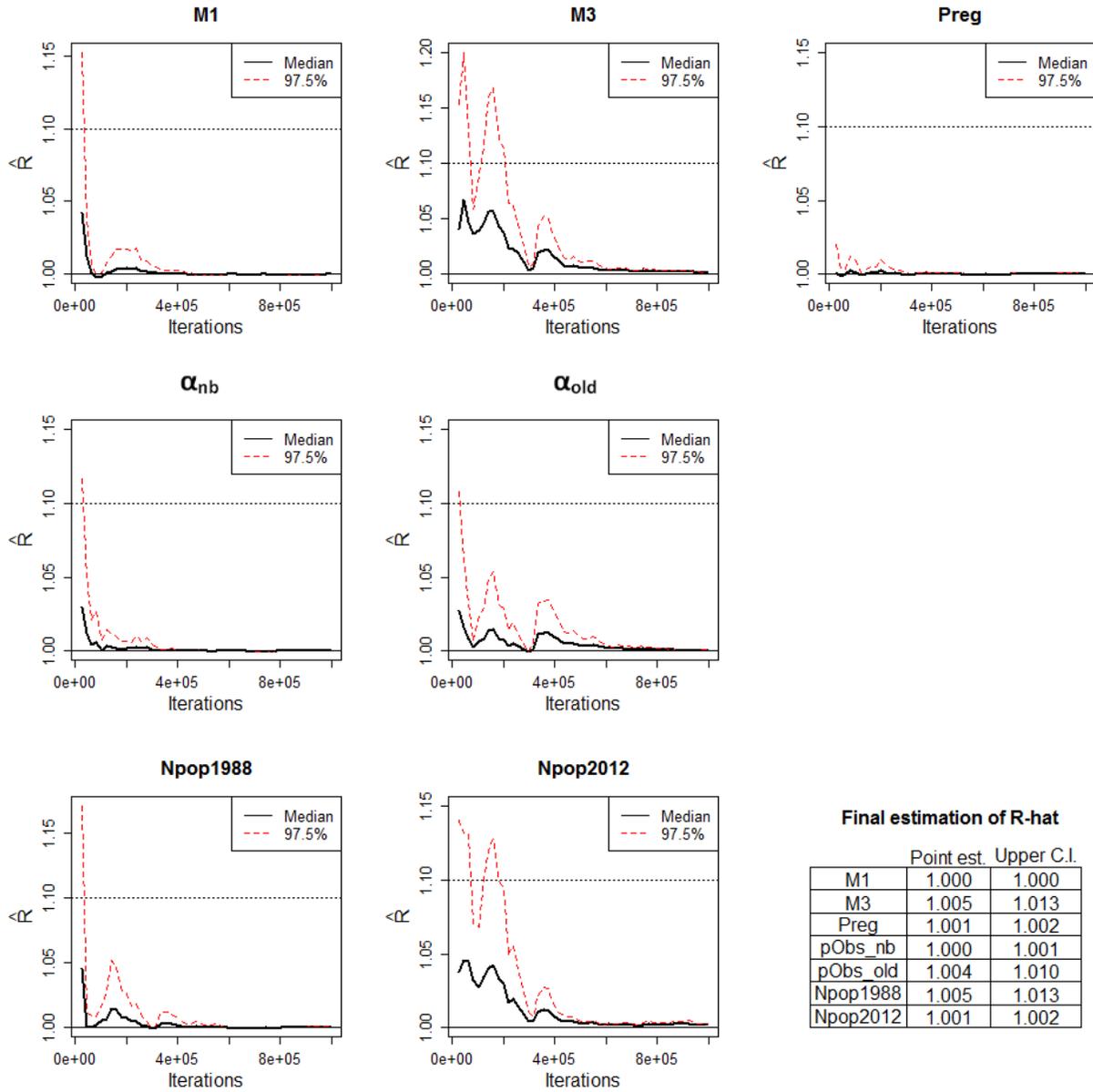
Figure 2. Evolution of the Gelman and Rubin statistic (also called R.hat) relative to the number of model iterations after the burn-in phase. Median (black bold line) and 97.5% CI (red dashed line) values of this statistic are presented for seven parameters of interest (M1, M3, Preg, α_{nb}, α_{old}, Npop1988, and Npop2012). A horizontal dotted line indicates the 1.1 threshold over which it is considered that chains did not converge (Gelman and Shirley 2011). See Table 1 for a description of variables.
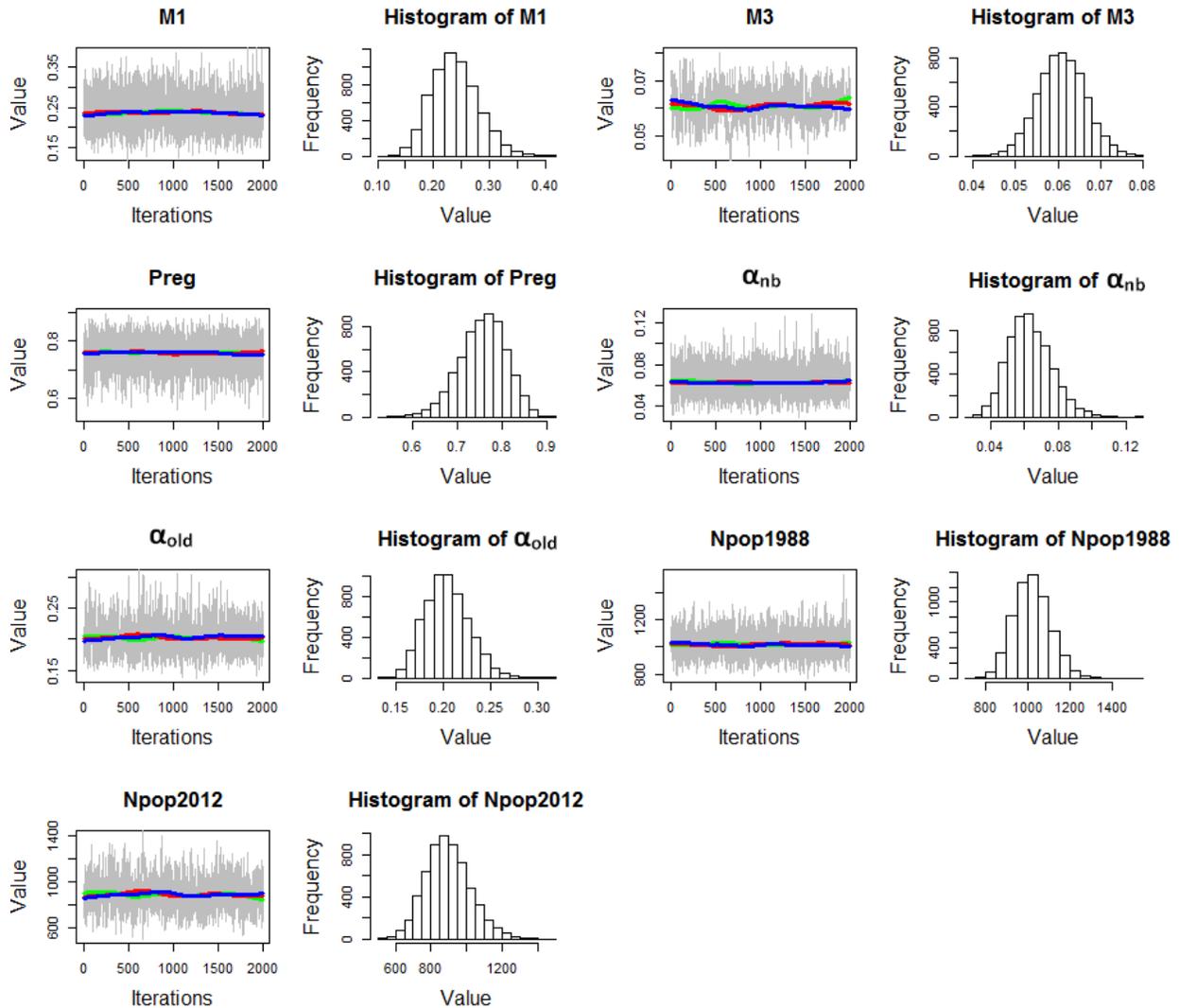
Figure 3. Trace plots and histogram for seven variables of interest (M1, M3, Preg, α_{nb}, α_{old}, Npop1988, and Npop2012). Trace plots present as grey lines the values of the 2000 samples extracted from three chains. Smoothed traces appear on the same graph as three colored lines (red, blue and green) showing good mixing and convergence. Histograms present the posterior distributions of the variables obtained from the 6000 samples (2000 by chain) combined. See Table 1 for a description of variables.
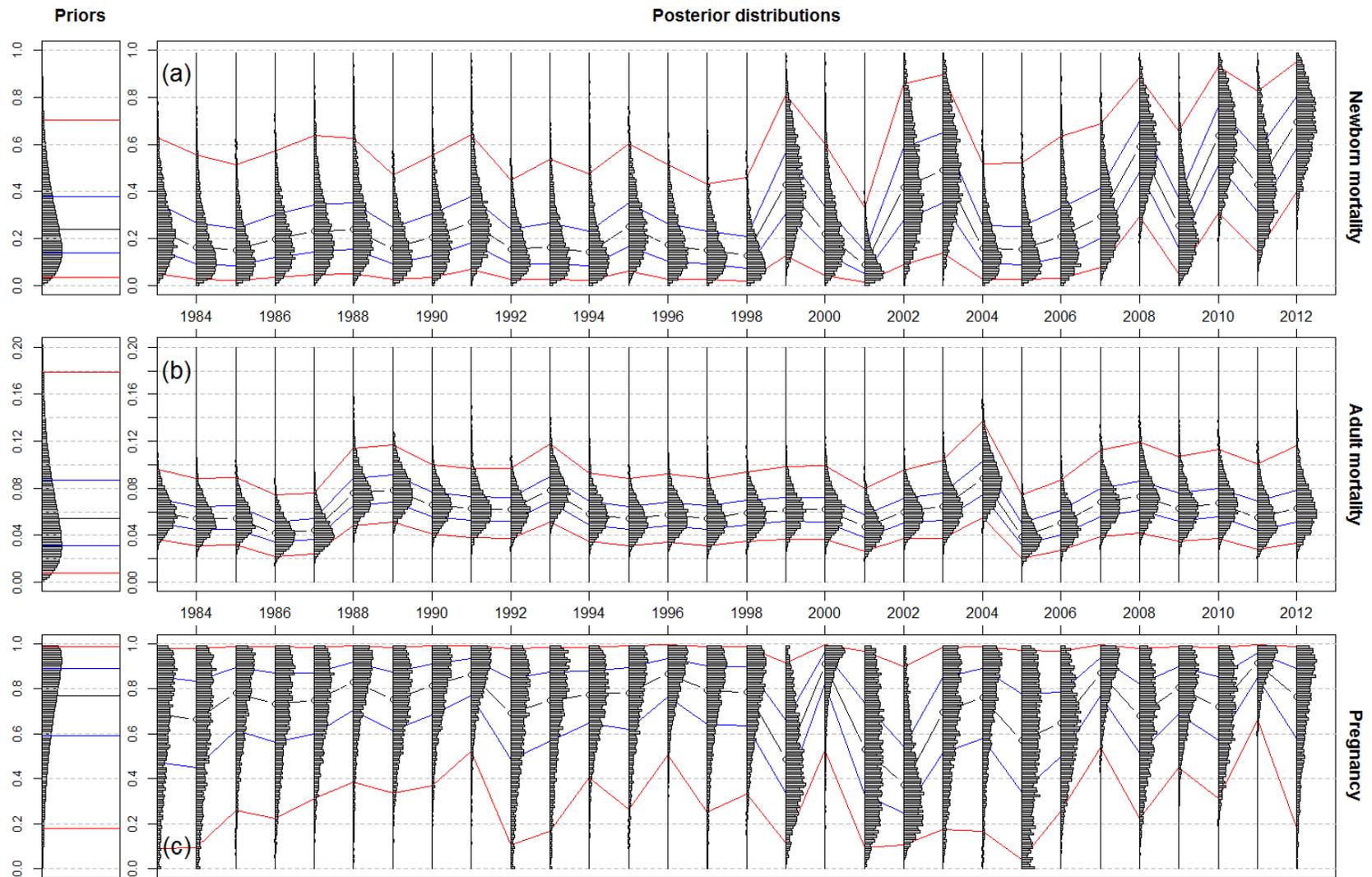
Figure 4. Posterior distributions of the newborn mortality (M_{nb}), the adult mortality (M_{adult}), the pregnancy rate (Pregnancy) and the probability of detecting carcasses of newborn (pObs Newborn) or older beluga (pObs Older), for each year of the "fitting period" (see material and methods). Prior distribution is also presented as a reference to identify when information is updated in the model. Median, 50th and 95th percentiles of each distribution are shown as black, blue and red lines respectively.
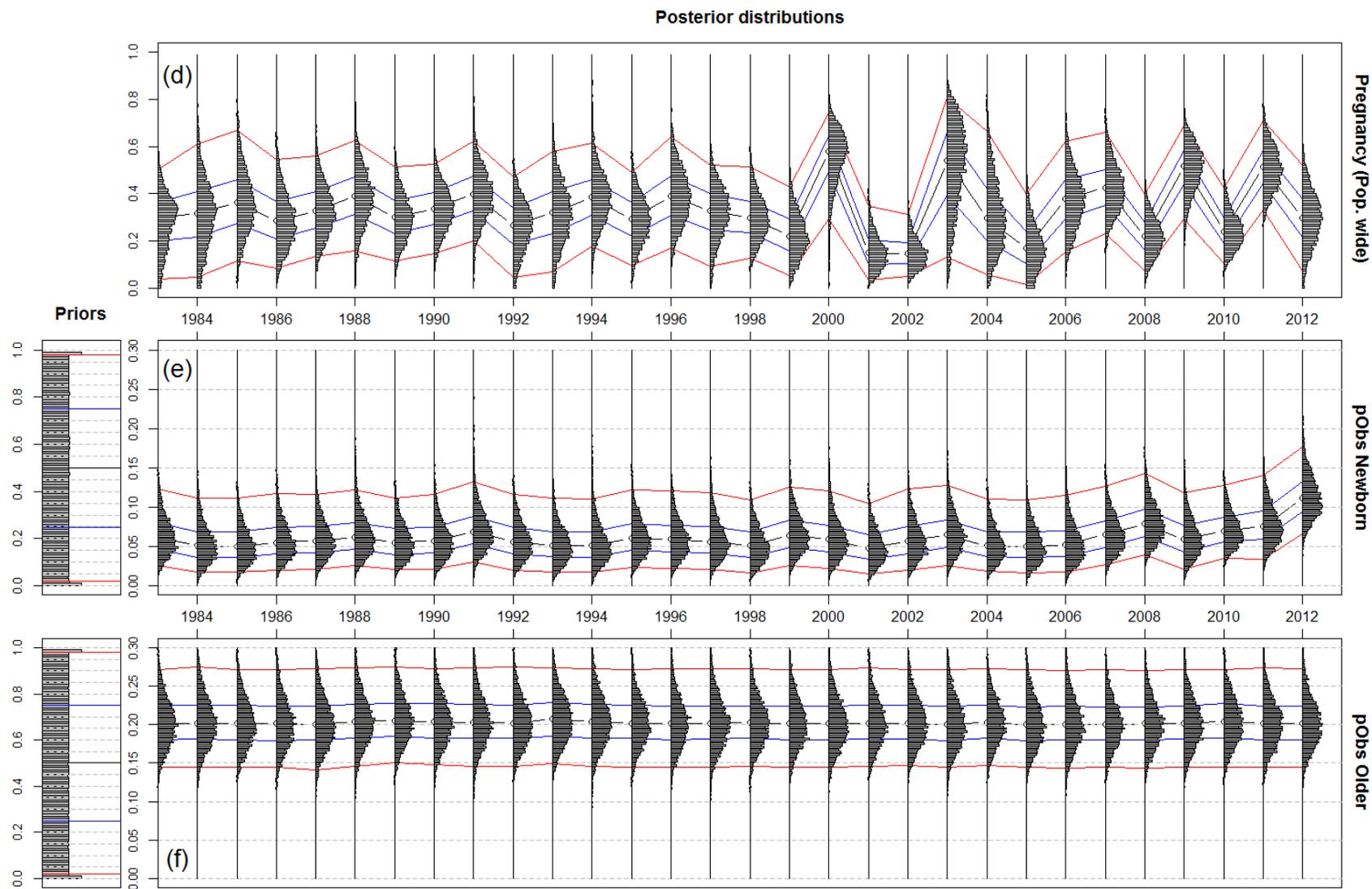
Figure 4 (continued). Note: scales for pObs prior and posterior distributions differ.
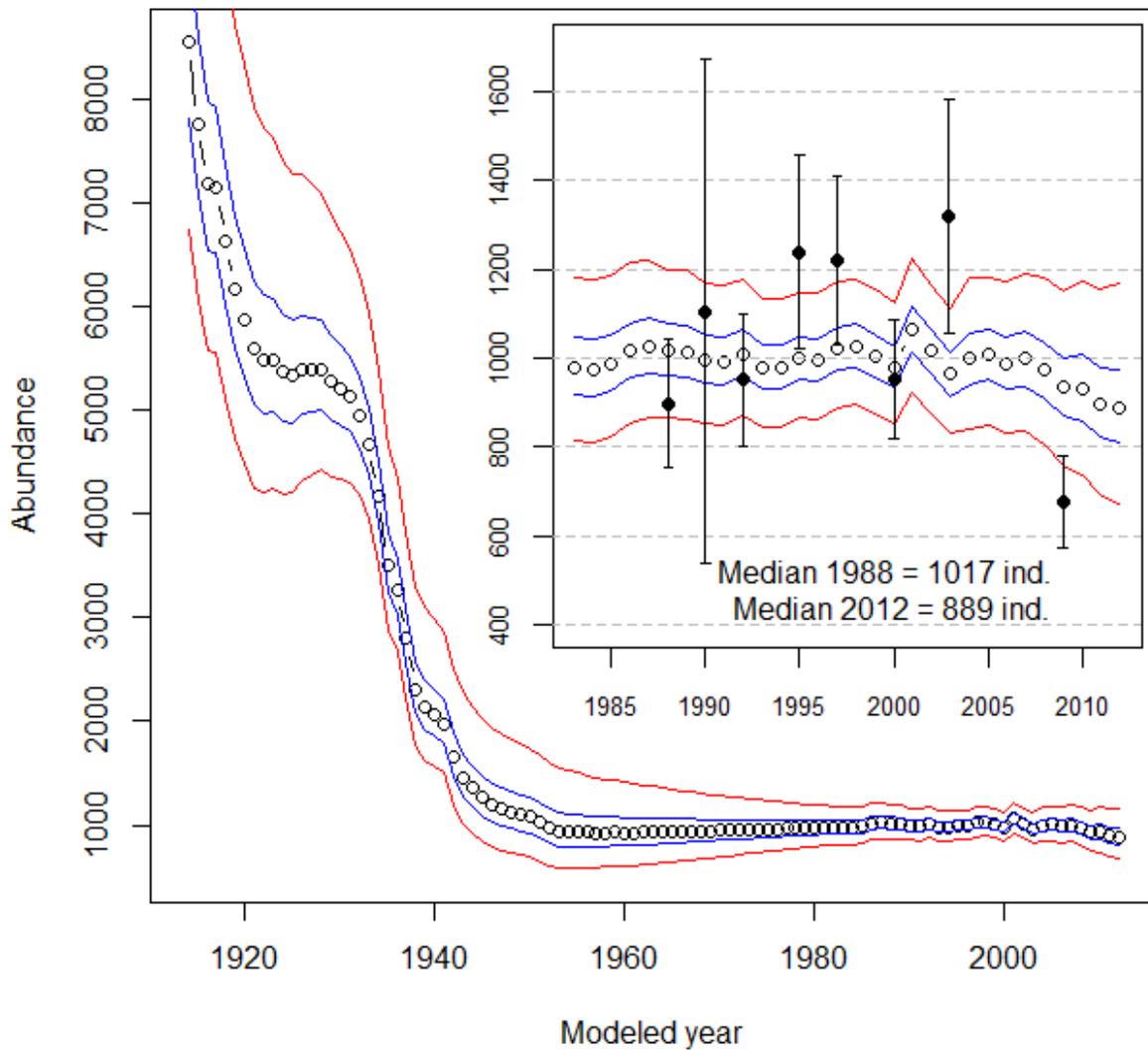
Figure 5. Evolution of the St. Lawrence beluga population size estimated by the population dynamics model for the period 1912-2012. Median values (black line with hollow points) along with 50 and 95% confidence intervals (blue and red lines respectively) are presented. An inset shows the period 1983-2012 including estimated mean population size (+/- SE) obtained from the photographic aerial surveys (Gosselin et al. 2014).Those values are one of the 4 datasets used to fit the model.
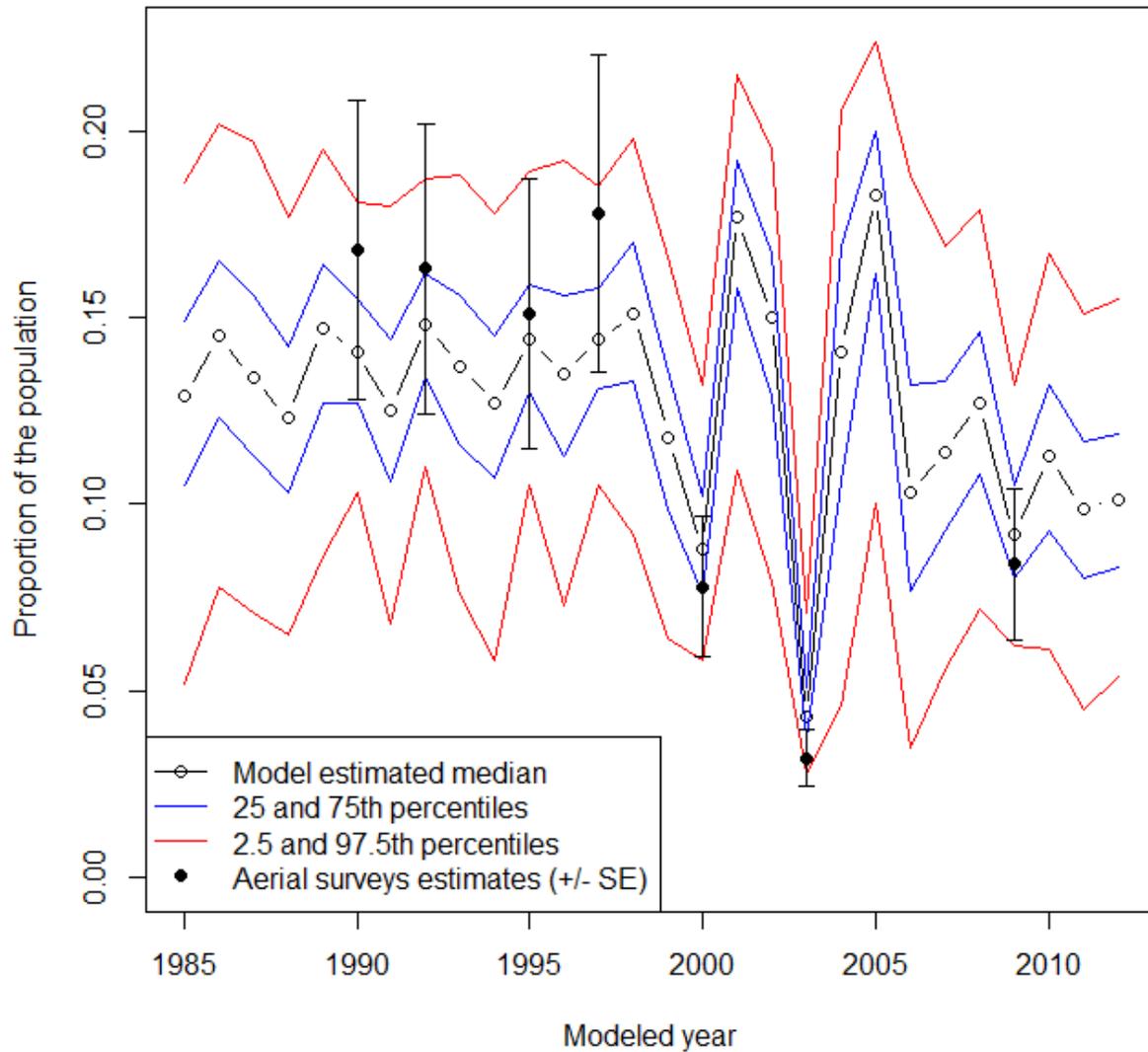
Figure 6. Evolution of the proportion of young (< 2 years old) in the St. Lawrence beluga population estimated by the population dynamics model. Median values (black line with hollow points) along with 50 and 95% confidence intervals (blue and red lines respectively) are presented. Proportions estimated from the photographic aerials surveys are also shown as black dots (Gosselin et al. 2014). Those values are one of the 4 datasets used to fit the model.
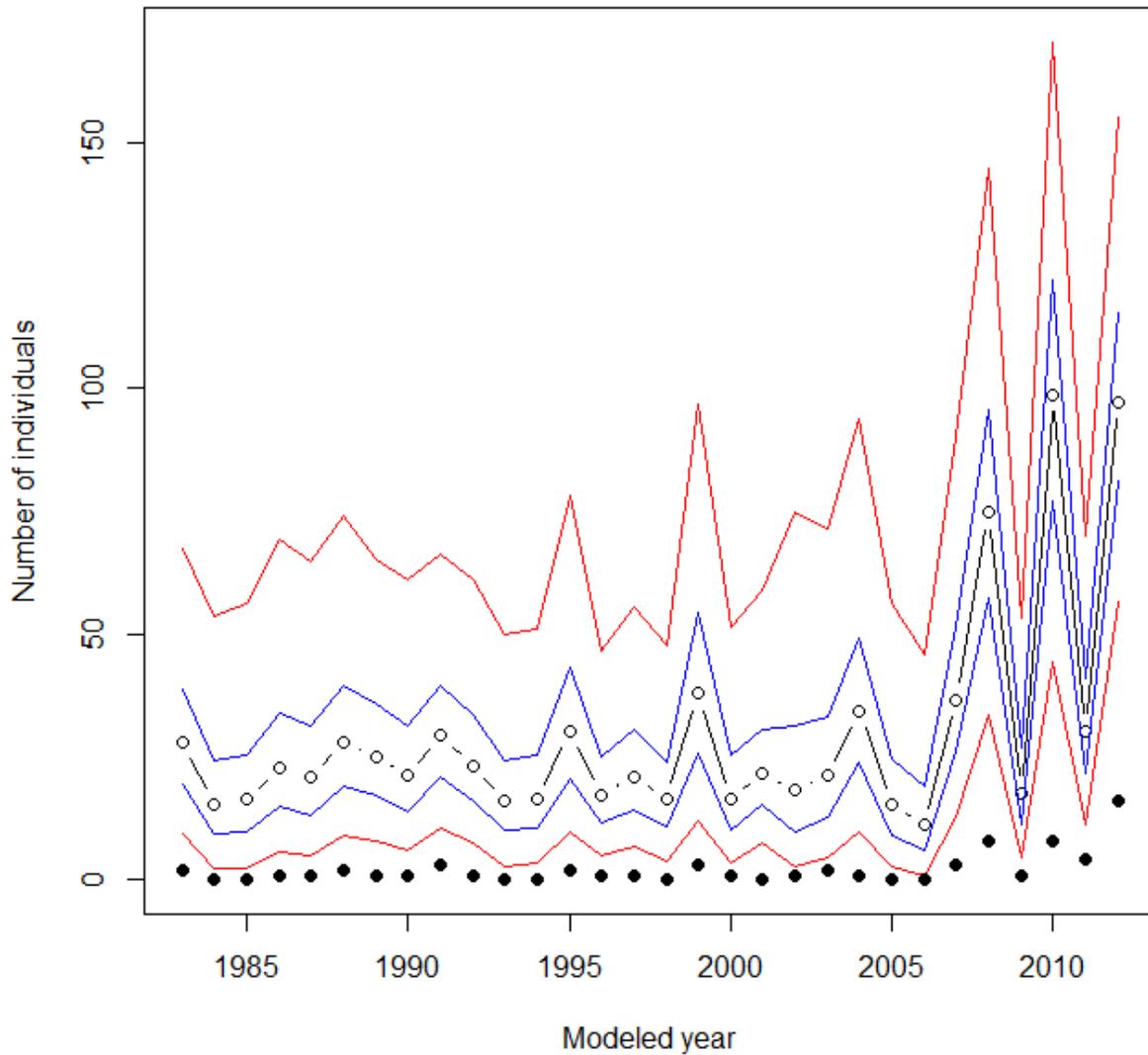
Figure 7. Evolution of the number of newborn beluga dying each year as estimated by the population dynamics model for the period 1983-2012. Median values (black line with hollow points) along with 50 and 95% confidence intervals (blue and red lines respectively) are presented. Number of beluga carcasses found each year is also shown as black dots (Lesage et al. 2014). Those values are one of the 4 datasets used to fit the model.
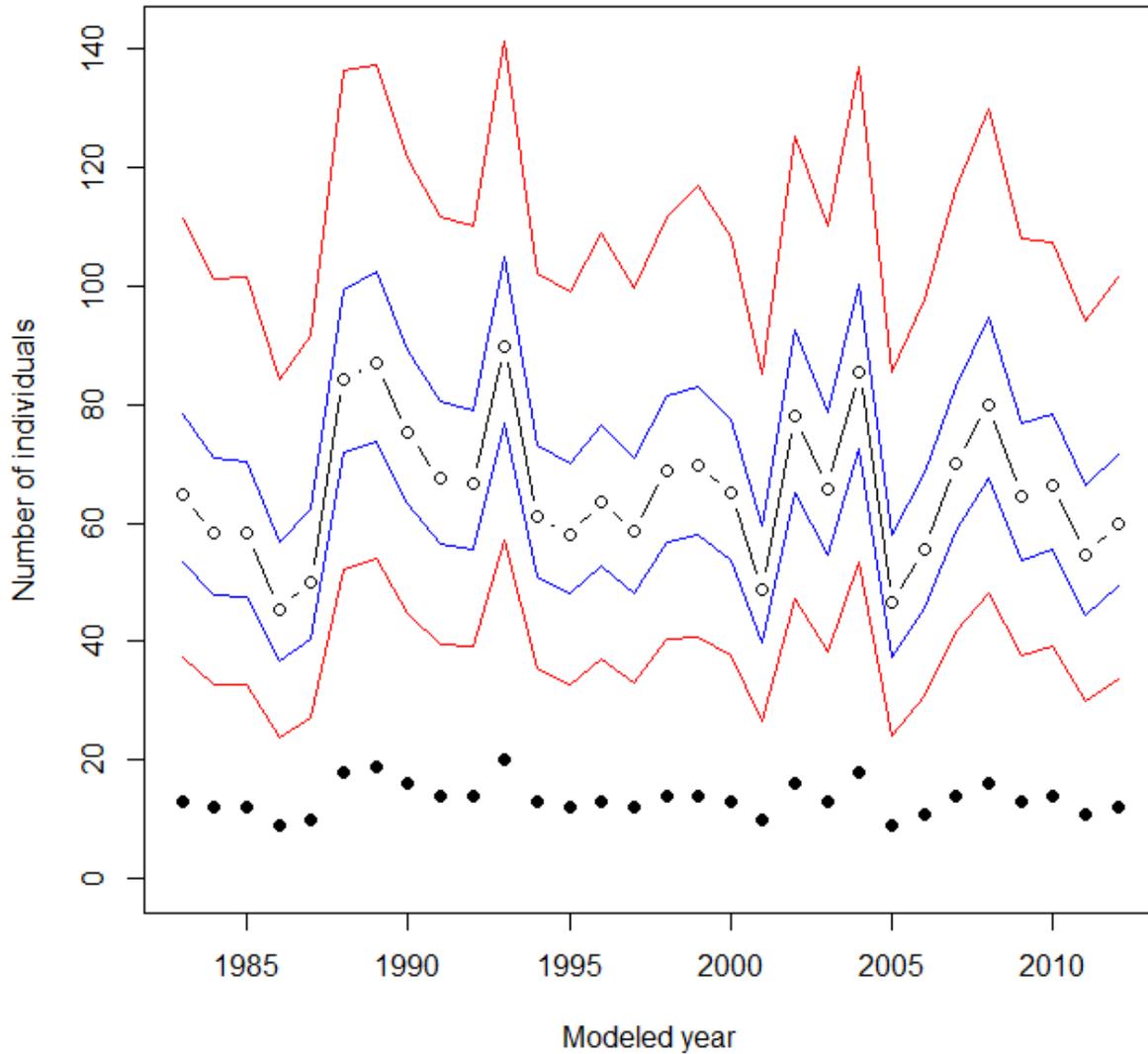
Figure 8. Evolution of the number of beluga aged 1 year and older dying each year as estimated by the population dynamics model for the period 1983-2012. Median values (black line with hollow points) along with 50 and 95% confidence intervals (blue and red lines respectively) are presented. Number of beluga carcasses found each year is also shown as black dots (Lesage et al. 2014). Those values are one of the 4 datasets used to fit the model.
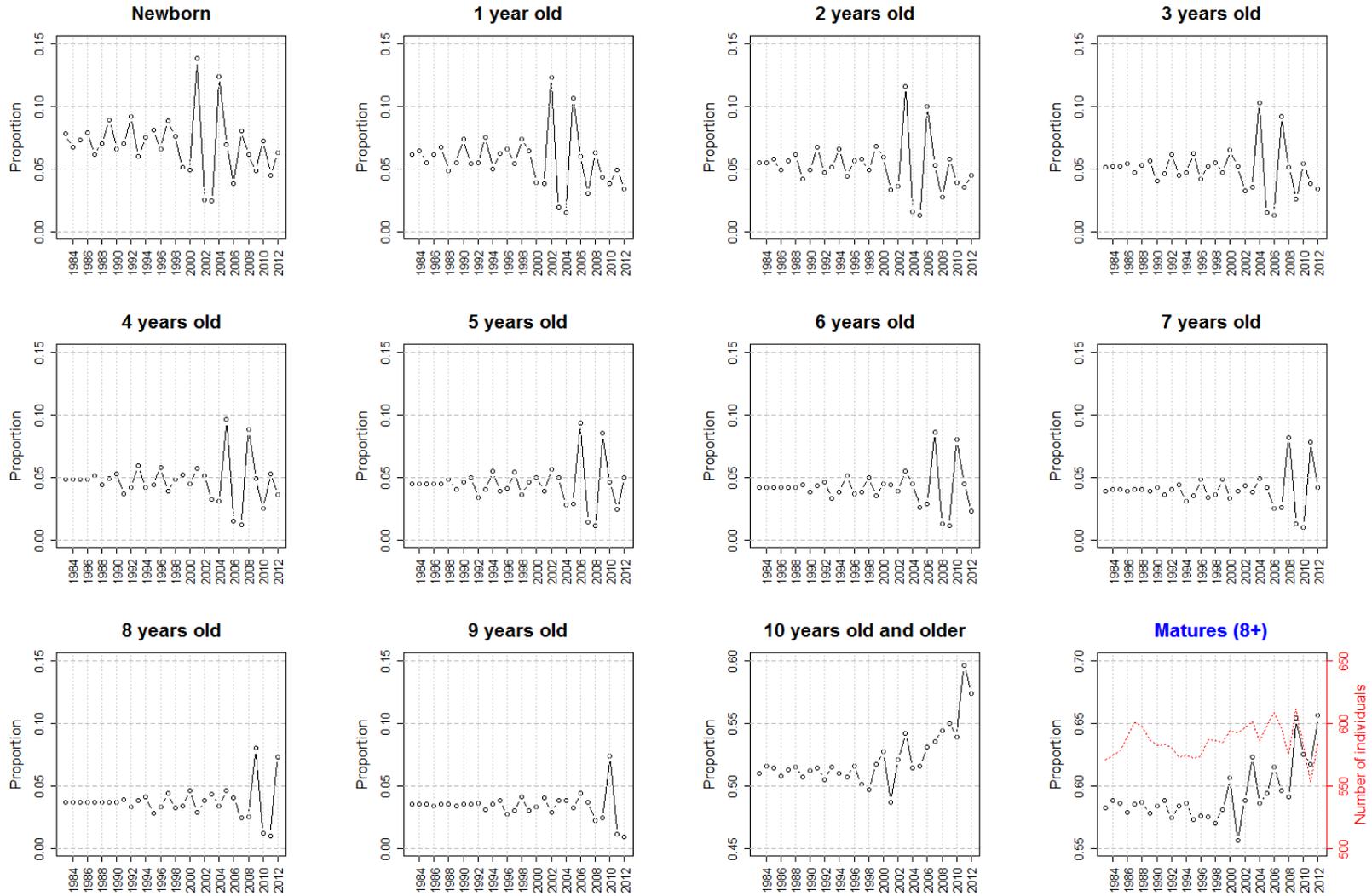
Figure 9. Model estimates of the evolution of the proportion of the St Lawrence beluga population (black line with hollow dots) occurring in the 11 age classes (see material and methods) over the period 1983-2012.The last graph shows the proportion (black line and hollow dots) and the number of individuals (red dotted line) considered mature (8 years old and older).

*Figure 10. Evolution of the St Lawrence beluga population age structure estimated by the population dynamic model for the period 1988-2012.
Note: Immature stage included individuals < 8 years old.*
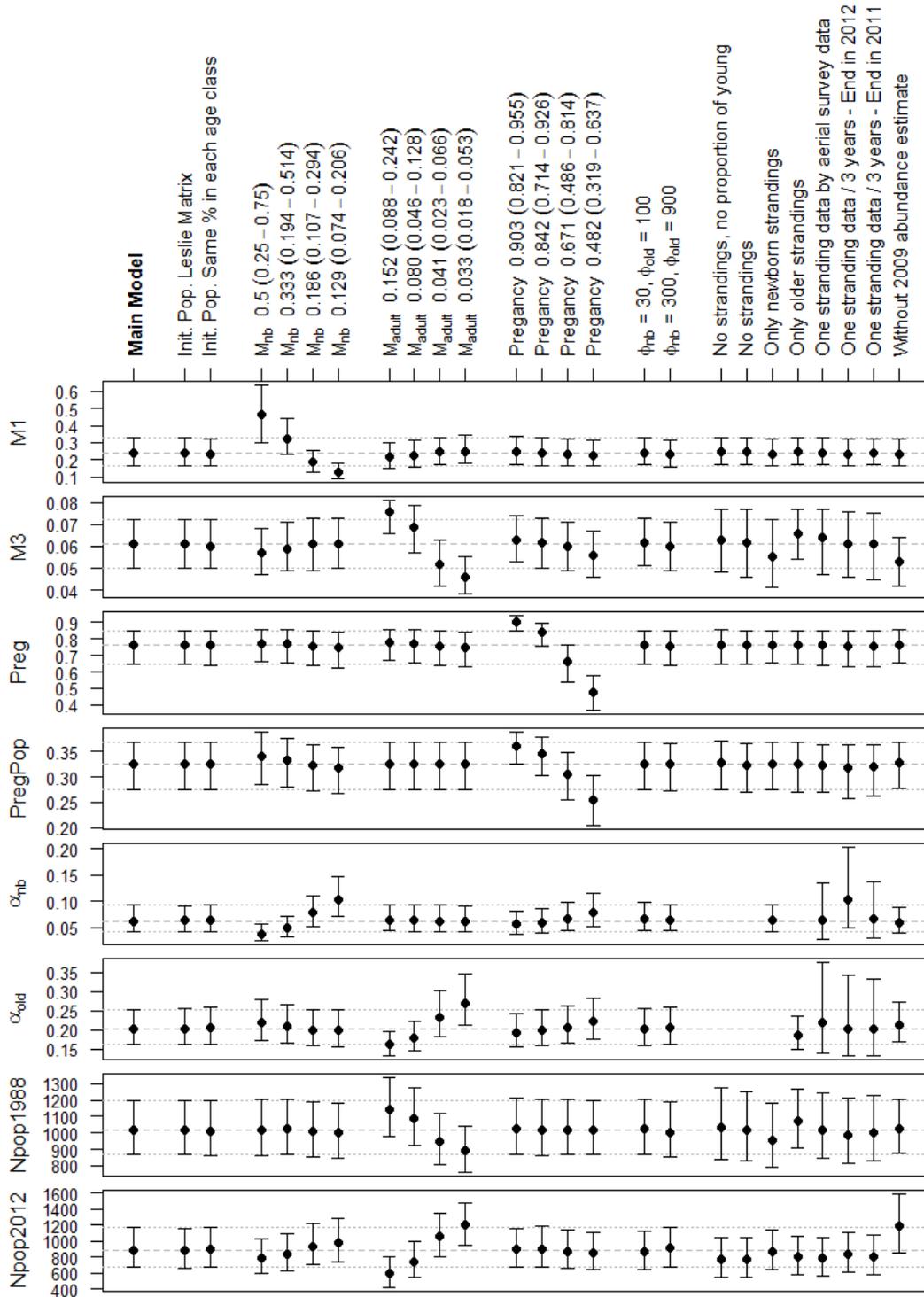
Figure 11. Sensitivity of the median estimates (black dots) of eight selected variables (M1, M3, Preg, PregPop, α_{nb}, α_{old}, Npop1988, and Npop2012) and their 95% CI (bars) to the initial population structure used in the model, to the prior distributions of M_{nb}, M_{adult}, and Pregnancy, to the value of φ_{nb}, and φ_{old} and finally to the type of dataset fitted in the model. For each variable considered, a grey dashed line and two grey dotted lines indicate as references the median and 95% confidence intervals obtained with the main model. See Table 1 for a description of variables.
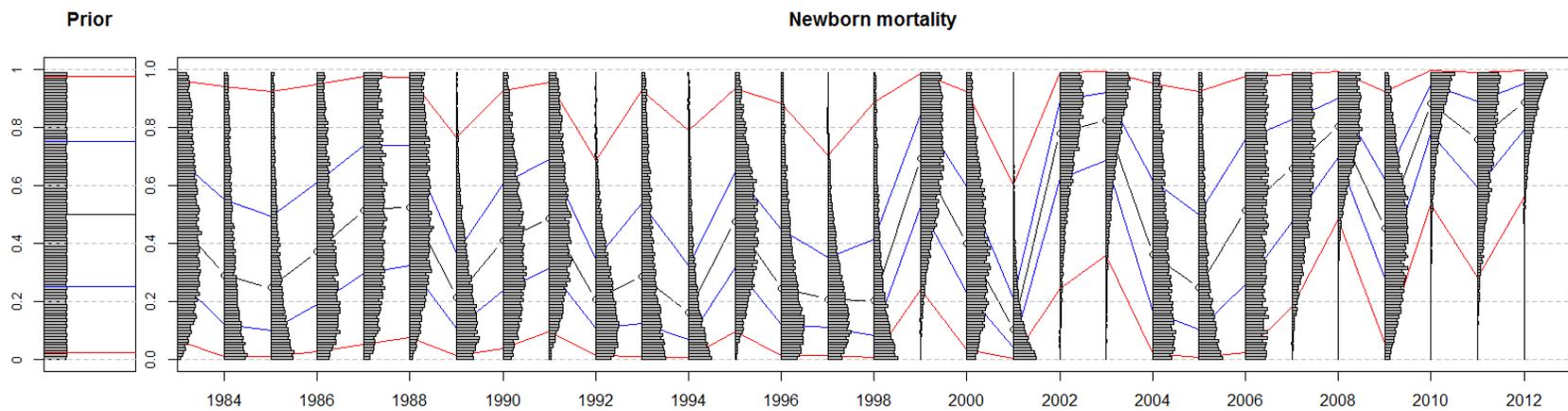
Figure 12. Posterior distributions of the annual newborn mortality for the period 1983-2012 compared to a non-informative uniform prior distribution. For several years (i.e. 1983, 1987, 1988, 2006), the prior distribution is not or only slightly updated.
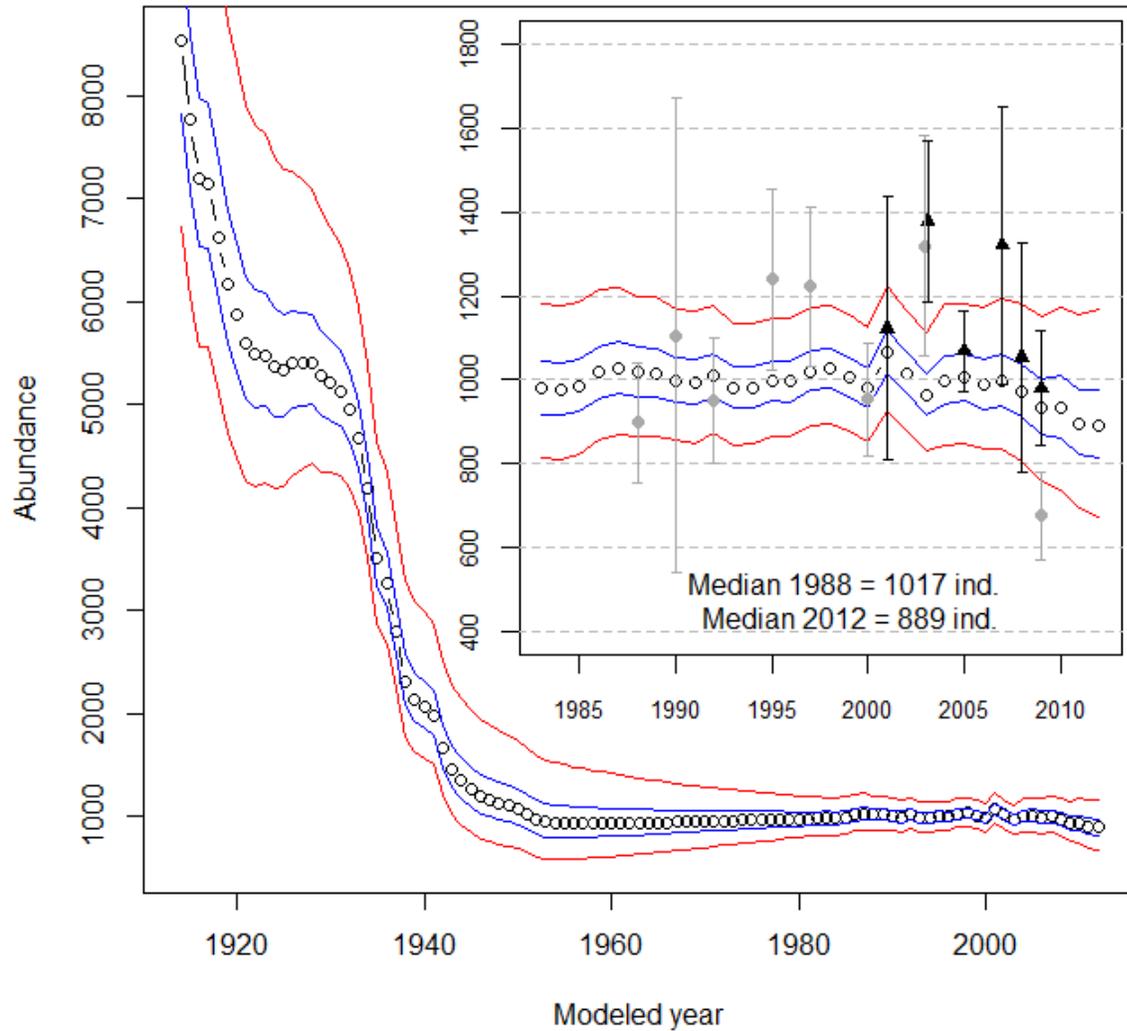
Figure 13. Superimposition of abundance estimates (▲, +/- SE) obtained from visual surveys (Gosselin et al. 2014) on the population trajectory estimated by the model. Fitted abundance estimates (●, +/- SE) obtained from photographic surveys are also shown.

Table A1. Output values (median and 95%CI), for eight variables of interest (M1, M3, Preg, PregPop, α$_{nb}$, α$_{old}$, Npop1988, and Npop2012, see Table 1 for a description of variables.), for sensibility tests involving changes in model priors and datasets used for the fitting. The main model priors and output values are indicated as a reference. These values are used to construct Figure 11.

		M1			M3			Preg			PregPop		
		2.5%	50%	97.5%	2.5%	50%	97.5%	2.5%	50%	97.5%	2.5%	50%	97.5%
Main Model		0.165	0.237	0.327	0.050	0.061	0.072	0.645	0.760	0.850	0.276	0.326	0.369
Init Pop. Mnb Madult Pregnancy pObs alpha nb pObs alpha old pObs phi nb pObs phi old	Burns and Seaman (1985) 0.239 (50%CI 0.138-0.375) 0.054 (50%CI 0.031-0.087) 0.769 (50%CI 0.588-0.891) 0.5 (50%CI 0.25-0.75) 0.5 (50%CI 0.25-0.75) 100 300												
Init Pop LeslieMatrix		0.165	0.237	0.327	0.050	0.061	0.072	0.646	0.760	0.849	0.276	0.326	0.368
Init Pop AllTheSameProp		0.165	0.235	0.324	0.050	0.060	0.072	0.643	0.762	0.850	0.275	0.326	0.367
Mnb beta(1,1)	0.5 (50%CI 0.25-0.75)	0.299	0.462	0.638	0.047	0.057	0.068	0.664	0.774	0.858	0.286	0.341	0.389
Mnb beta(2, gamma(4,1))	0.333 (50%CI 0.194-0.514)	0.230	0.325	0.444	0.049	0.059	0.071	0.654	0.768	0.854	0.281	0.333	0.376
Mnb beta(2, gamma(8,1))	0.186 (50%CI 0.107-0.294)	0.128	0.184	0.255	0.049	0.061	0.073	0.639	0.755	0.846	0.272	0.322	0.363
Mnb beta(2,gamma(12,1))	0.129 (50%CI 0.074-0.206)	0.088	0.127	0.177	0.050	0.061	0.073	0.626	0.747	0.841	0.268	0.317	0.357
Madult beta(2, gamma(10,1))	0.152 (50%CI 0.088-0.242)	0.151	0.218	0.298	0.066	0.076	0.081	0.669	0.776	0.860	0.275	0.325	0.367
Madult beta(2, gamma(20,1))	0.080 (50%CI 0.046-0.128)	0.158	0.228	0.316	0.057	0.069	0.079	0.654	0.768	0.856	0.276	0.326	0.367
Madult beta(2, gamma(40,1))	0.041 (50%CI 0.023-0.066)	0.171	0.244	0.333	0.042	0.052	0.063	0.638	0.754	0.845	0.275	0.326	0.367
Madult beta(2, gamma(50,1))	0.033(50%CI 0.018-0.053)	0.176	0.250	0.344	0.038	0.046	0.055	0.629	0.747	0.841	0.274	0.325	0.367
Preg beta(gamma(10,1), gamma(20,15))	0.903 (50%CI 0.821-0.955)	0.169	0.244	0.337	0.053	0.063	0.074	0.852	0.901	0.939	0.326	0.360	0.389
Preg beta(gamma(6,1), gamma(20,15))	0.842 (50%CI 0.714-0.926)	0.167	0.239	0.330	0.050	0.062	0.073	0.754	0.837	0.898	0.302	0.345	0.379
Preg beta(gamma(4,1), gamma(20,10))	0.671 (50%CI 0.486-0.814)	0.163	0.233	0.322	0.049	0.060	0.071	0.540	0.660	0.761	0.254	0.305	0.348
Preg beta(gamma(4,1), gamma(20,5))	0.482 (50%CI 0.319-0.637)	0.161	0.228	0.314	0.046	0.056	0.067	0.370	0.475	0.579	0.205	0.256	0.302
pObs phi nb 30 and pObs phi old 100		0.170	0.243	0.333	0.051	0.062	0.073	0.647	0.760	0.849	0.276	0.326	0.367
pObs phi nb 300 and pObs phi old 900		0.160	0.229	0.318	0.049	0.060	0.071	0.638	0.758	0.849	0.272	0.324	0.366
No Strandings - No Prop. Young		0.172	0.245	0.330	0.048	0.063	0.077	0.650	0.765	0.854	0.276	0.329	0.371
No Strandings		0.172	0.244	0.331	0.046	0.062	0.077	0.645	0.760	0.850	0.270	0.323	0.366
Only Newborn Strandings		0.164	0.234	0.323	0.041	0.055	0.072	0.653	0.764	0.852	0.275	0.326	0.367
Only Older Strandings		0.173	0.245	0.332	0.054	0.066	0.077	0.644	0.760	0.849	0.270	0.324	0.367
One Stranding Data By Aerial Survey Data		0.169	0.240	0.327	0.047	0.064	0.077	0.643	0.760	0.850	0.270	0.322	0.364
One Stranding Data Every 3 years - End In 2012		0.164	0.235	0.322	0.046	0.061	0.076	0.635	0.756	0.849	0.258	0.317	0.364
One Stranding Data Every 3 years - End in 2011		0.169	0.239	0.325	0.045	0.061	0.075	0.634	0.752	0.845	0.263	0.320	0.364
Without 2009 abundance estimate		0.164	0.234	0.321	0.042	0.053	0.064	0.654	0.766	0.854	0.278	0.327	0.368

The left groups are labeled *Priors* (Init Pop LeslieMatrix … pObs phi nb 300 and pObs phi old 900) and *Datasets* (No Strandings - No Prop. Young … Without 2009 abundance estimate).

		α_nb			α_old			Pop1988			Pop2012		
		2.5%	50%	97.5%	2.5%	50%	97.5%	2.5%	50%	97.5%	2.5%	50%	97.5%
Main Model		0.041	0.062	0.092	0.163	0.202	0.253	866	1017	1200	672	889	1167
Init Pop.	Burns and Seaman (1985)												
Mnb	0.239 (50%CI 0.138-0.375)												
Madult	0.054 (50%CI 0.031-0.087)												
Pregnancy	0.769 (50%CI 0.588-0.891)												
pObs alpha nb	0.5 (50%CI 0.25-0.75)												
pObs alpha old	0.5 (50%CI 0.25-0.75)												
pObs phi nb	100												
pObs phi old	300												
Priors Init Pop LeslieMatrix		0.041	0.063	0.091	0.163	0.202	0.255	868	1019	1193	668	892	1166
Init Pop AllTheSameProp		0.042	0.063	0.092	0.163	0.205	0.258	859	1011	1192	681	904	1168
Mnb beta(1,1)	0.5 (50%CI 0.25-0.75)	0.024	0.037	0.057	0.174	0.220	0.280	865	1015	1200	601	792	1036
Mnb beta(2, gamma(4,1))	0.333 (50%CI 0.194-0.514)	0.031	0.048	0.071	0.167	0.209	0.265	866	1023	1207	631	841	1097
Mnb beta(2, gamma(8,1))	0.186 (50%CI 0.107-0.294)	0.052	0.077	0.111	0.161	0.201	0.254	854	1007	1191	704	940	1229
Mnb beta(2,gamma(12,1))	0.129 (50%CI 0.074-0.206)	0.070	0.103	0.146	0.158	0.199	0.251	847	1000	1179	743	988	1283
Madult beta(2, gamma(10,1))	0.152 (50%CI 0.088-0.242)	0.043	0.064	0.093	0.133	0.162	0.197	978	1144	1334	424	600	814
Madult beta(2, gamma(20,1))	0.080 (50%CI 0.046-0.128)	0.042	0.063	0.092	0.145	0.179	0.224	922	1085	1274	544	742	991
Madult beta(2, gamma(40,1))	0.041 (50%CI 0.023-0.066)	0.041	0.062	0.092	0.184	0.233	0.301	805	948	1119	810	1056	1347
Madult beta(2, gamma(50,1))	0.033(50%CI 0.018-0.053)	0.041	0.062	0.091	0.212	0.268	0.344	763	892	1043	953	1201	1478
Preg beta(gamma(10,1), gamma(20,15))	0.903 (50%CI 0.821-0.955)	0.036	0.055	0.080	0.156	0.194	0.243	869	1024	1208	676	898	1166
Preg beta(gamma(6,1), gamma(20,15))	0.842 (50%CI 0.714-0.926)	0.039	0.058	0.086	0.160	0.199	0.252	862	1017	1201	677	904	1184
Preg beta(gamma(4,1), gamma(20,10))	0.671 (50%CI 0.486-0.814)	0.044	0.066	0.097	0.165	0.207	0.261	867	1020	1206	661	876	1140
Preg beta(gamma(4,1), gamma(20,5))	0.482 (50%CI 0.319-0.637)	0.052	0.078	0.114	0.177	0.223	0.283	865	1015	1200	648	854	1111
pObs phi nb 30 and pObs phi old 100		0.043	0.066	0.098	0.161	0.203	0.256	865	1023	1208	644	863	1134
pObs phi nb 300 and pObs phi old 900		0.044	0.064	0.093	0.164	0.205	0.258	853	1005	1186	684	914	1178
Datasets No Strandings - No Prop. Young			NA			NA		841	1029	1271	555	776	1041
No Strandings			NA			NA		827	1013	1253	552	777	1048
Only Newborn Strandings		0.042	0.063	0.093		NA		788	957	1177	645	874	1145
Only Older Strandings			NA		0.150	0.187	0.235	909	1071	1263	588	806	1067
One Stranding Data By Aerial Survey Data		0.028	0.063	0.135	0.139	0.219	0.375	845	1019	1243	564	788	1050
One Stranding Data Every 3 years - End In 2012		0.050	0.102	0.203	0.132	0.204	0.341	812	987	1208	613	837	1108
One Stranding Data Every 3 years - End in 2011		0.029	0.065	0.137	0.132	0.202	0.333	829	1002	1226	580	806	1083
Without 2009 abundance estimate		0.039	0.059	0.088	0.169	0.213	0.272	874	1027	1207	857	1187	1597

APPENDIX 2

Effects of selecting various datasets as inputs to the model on estimated population trajectory.
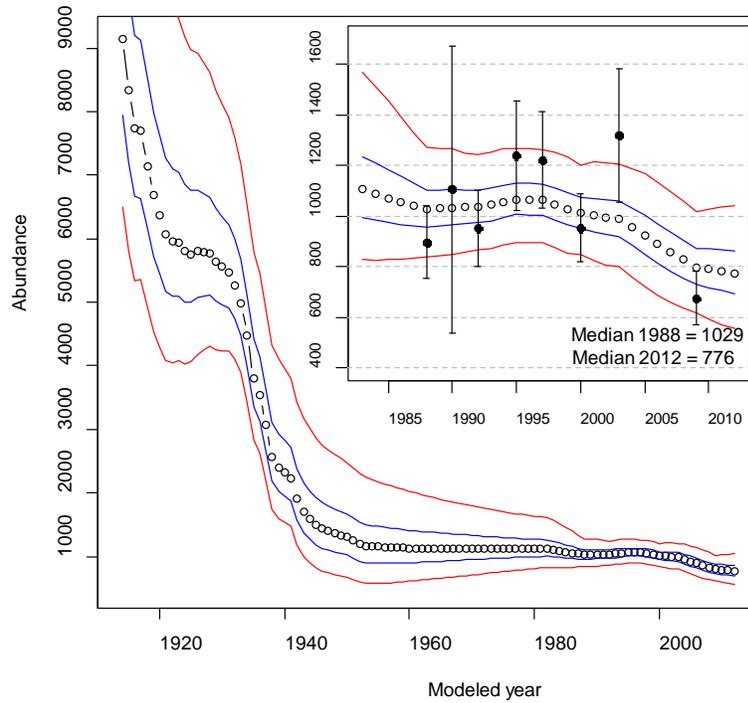
Figure A2-1. Population trajectory estimated from the model fitted only to the abundance estimates obtained from the aerial surveys (Gosselin et al. 2014).
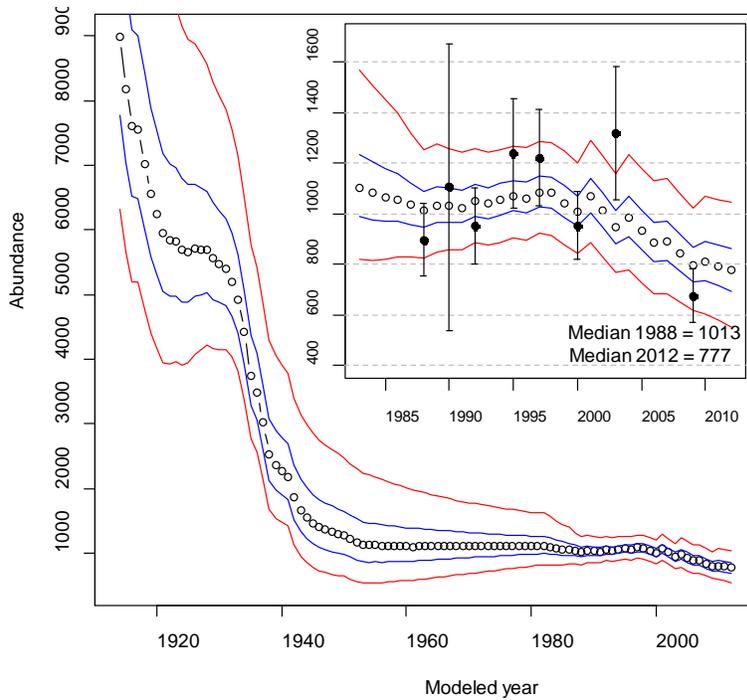
Figure A2-2. Population trajectory estimated from the model fitted to the abundance estimates and the proportion of young (newborns + yearlings) obtained from the aerial surveys (Gosselin et al. 2014).
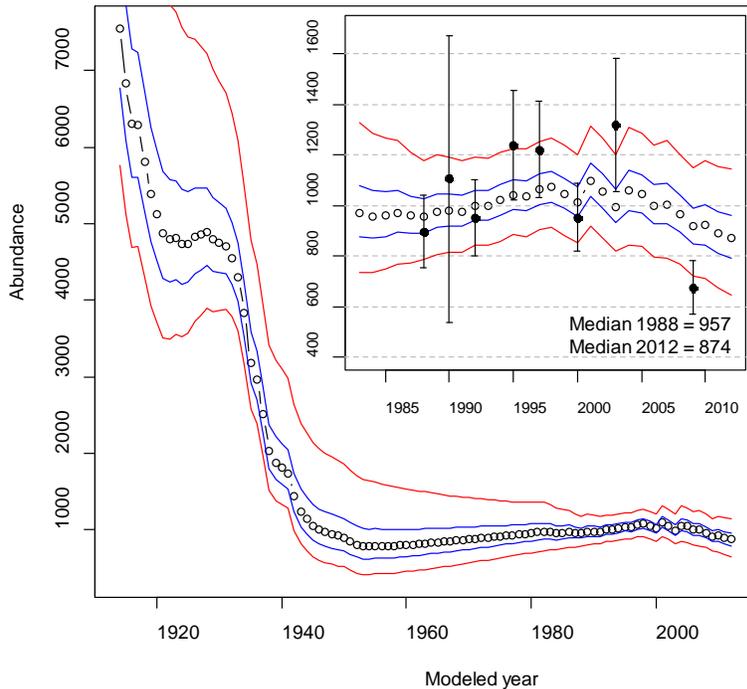
Figure A2-3. Population trajectory estimated from the model fitted to the abundance estimates and the proportion of young (newborns + yearlings) obtained from the aerial surveys (Gosselin et al. 2014) and the carcass data for newborns (Lesage et al. 2014).
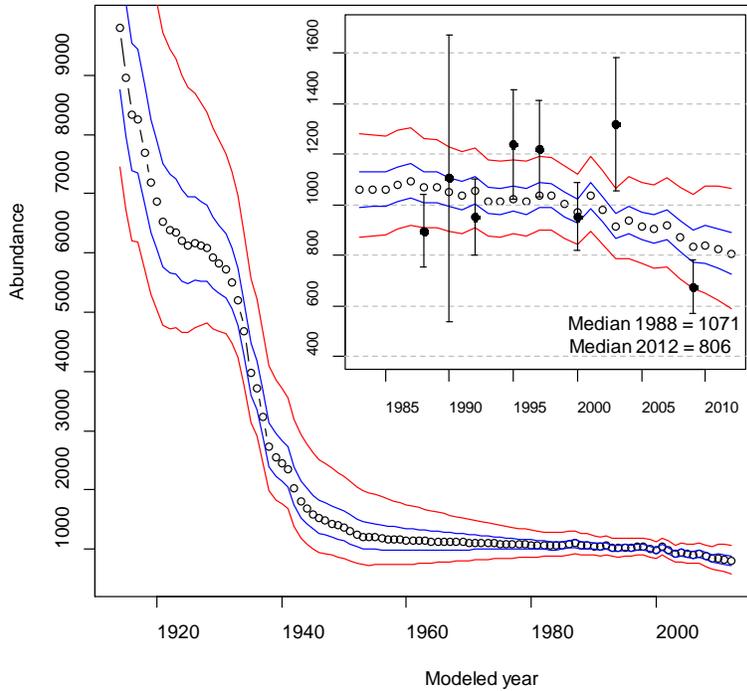
Figure A2-4. Population trajectory estimated from the model fitted to the abundance estimates and the proportion of young (newborns + yearlings) obtained from the aerial surveys (Gosselin et al. 2014) and the carcass data for older beluga (1-year-old and older, Lesage et al. 2014).
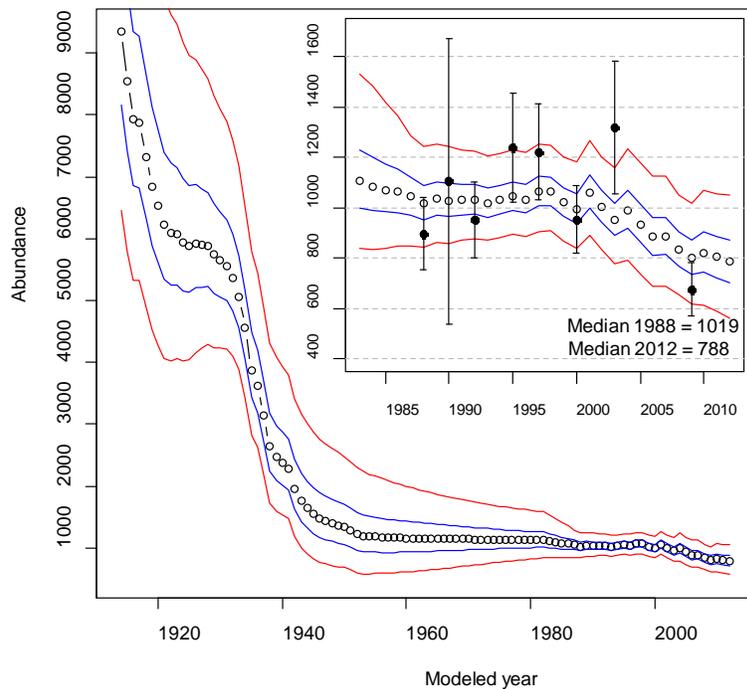
Figure A2-5. Population trajectory estimated from the model using carcass data only in the years when an aerial survey was conducted (Gosselin et al. 2014, Lesage et al. 2014).
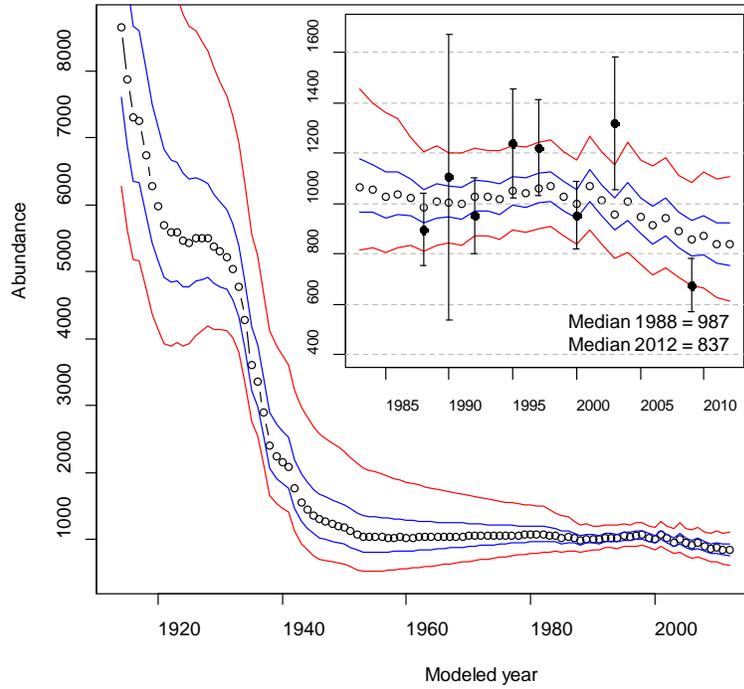
Figure A2-6. Population trajectory estimated from the model using carcass data sampled every 3 years and ending in 2012 (Lesage et al. 2014).
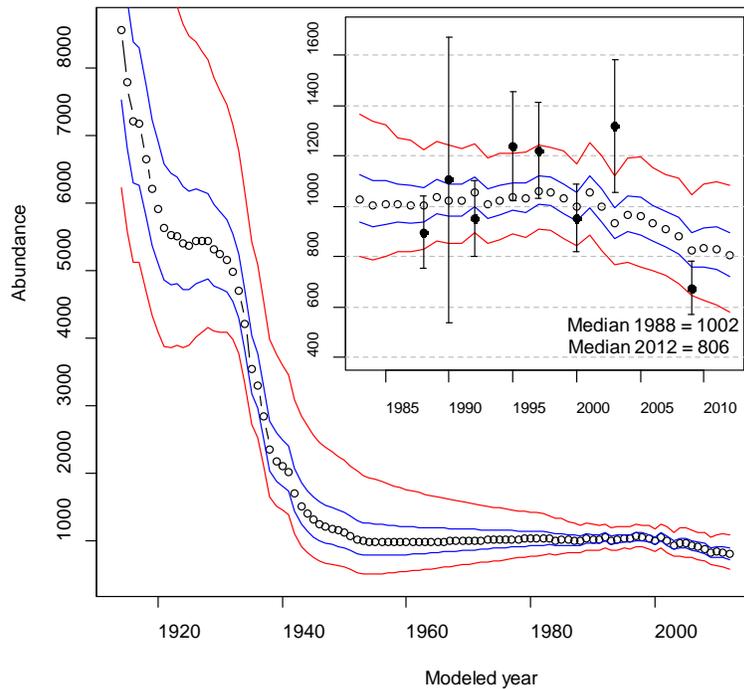
Figure A2-7. Population trajectory estimated from the model using carcass data sampled every 3 years and ending in 2011 (Lesage et al. 2014).
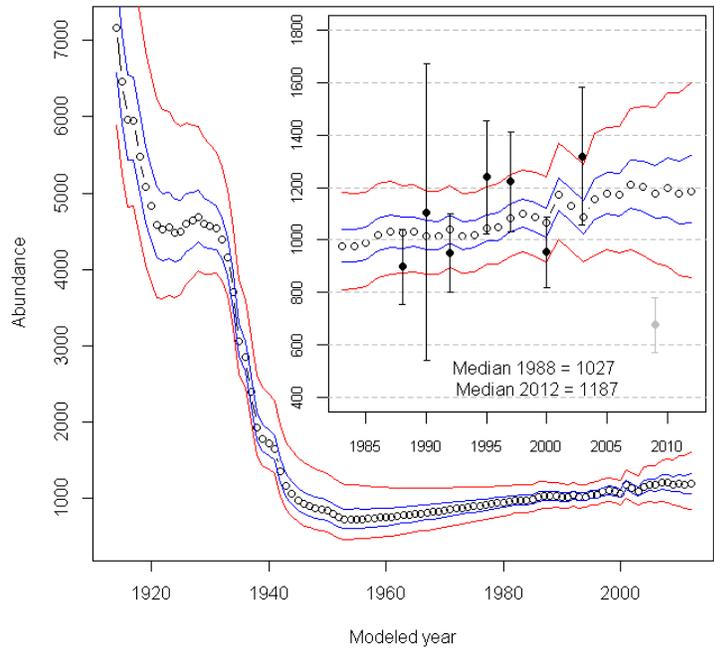
Figure A2-8. Population trajectory estimated from the model without fitting the 2009 abundance estimate (Gosselin et al. 2014).