Insights into processes of population decline using an integrated population model: The case of the St. Lawrence Estuary beluga (Delphinapterus leucas)

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Abstract

Integrated population models combine data from several sources into a single model to allow the simultaneous estimation of demographic parameters and the prediction of population trajectories. They are especially useful when survey data alone are insufficient to estimate precise vital rates and abundance, and to understand mechanisms of population growth and decline. The St. Lawrence Estuary (SLE) beluga population was depleted by intensive hunting over the past century, and had declined to 1000 individuals or less when it was afforded protection in 1979. Despite protective measures, the SLE population has shown no signs of recovery. Low abundance estimates and high calf mortalities observed in recent years have raised concerns as to its current status. An age-structured Bayesian model was used to describe population dynamics by integrating information from two different monitoring programs. The model included information on population size and proportion of young (<2 years-old) obtained from seven photographic aerial surveys flown between 1990 and 2009, and mortalities documented annually 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 belugas. The population then declined to 889 individuals (95%CI 672–1167) in 2012. Although neither dataset on its own could explain this decline, the integrated model was able to shed light on the internal processes involved. Results suggest substantial changes in population dynamics and age structure, moving from a stable period (1984–1998) characterized by a 3-year calving cycle and a population composed of 7.5% newborns and 42% immature individuals, to an unstable state (1999–2012) characterized by a 2-year calving cycle, high newborn mortality and a declining proportion of newborns and immatures (respectively, 6 and 33% in 2012). Independent indices of abundance, population age structure and calf production match model predictions, thus increasing our confidence in its conclusions. The lack of recovery, high adult mortality (6%) and highly variable newborn survival further increase concerns about this population.

1. Introduction

Identifying population declines and their underlying processes is one of the central paradigms in conservation biology (Caughley, 1994). Unprecedented reductions in abundance of numerous species worldwide have hastened efforts to identify population trends and extinction risks (Mace et al., 2008). After heavy exploitation throughout history, many marine mammals appear to have benefitted from a shift from resource exploitation toward wildlife conservation (Magera et al., 2013), with some formerly depleted populations showing remarkable recoveries (Best, 1993; Gerber and Hilborn, 2001; Lotze et al., 2011). Other populations, however, have remained at low abundance levels or have continued to decline despite management measures (Hobbs et al., 2000; Wade et al., 2007). Effective conservation actions require a better understanding of the internal mechanisms responsible for such recovery failures.

Monitoring of wildlife populations usually relies on accurate assessment of their abundance and trends (Krebs, 1994; Morris and Doak, 2002). Unfortunately, detectability issues during field surveys (e.g. availability and perception biases; Buckland et al., 2001) often lead to highly uncertain abundance estimates (Cooke, 1999;
Long-lived animals are also difficult to monitor because of the time-frame necessary to evaluate their life-history process (Clutton-Brock and Sheldon, 2010). This results in low power to detect significant changes in population trends in time for management actions (Taylor et al., 2007; Kéry and Royle, 2010). Moreover, monitoring population size alone does not provide sufficient information for management when causes of decline are unknown (Caughley, 1994). An alternative approach is to monitor reproductive and survival rates (Fowler and Sinniff, 1992; Chivers, 1999; Caswell, 2001) and use demographic analysis to explore their relationship to population growth (Norris, 2004). Data on declining or small populations can be scarce, however, because sample size is naturally low and researchers hesitate to catch and mark individuals (Beissinger and McCullough, 2002). Consequently, longitudinal data necessary to model population viability are often not available (Heppell et al., 2000; Morris and Doak, 2002).

Recently developed integrated population models (IPMs) attempt to overcome drawbacks associated with the traditional approach of treating the population and demographic data separately, by combining all data into a single model (Besbeas et al., 2002, 2005; Brooks et al., 2004). This approach allows the simultaneous estimation of demographic parameters and the prediction of population trajectories (Schaub and Abadi, 2011). Because population counts also contain demographic information, IPMs provide considerably more precise estimates of demographic parameters (Schaub and Abadi, 2011) and allow estimation of parameters for which no explicit data are available (Besbeas et al., 2002). This modelling framework also provides the required flexibility to link individual-level changes in demographic processes to population-level effects.

The beluga (Delphinapterus leucas) is a medium-sized cetacean with a northern circumpolar distribution. The St. Lawrence Estuary (SLE) population of beluga is located at the southernmost limit of the species range, which coincides with the southern limit of the seasonal pack ice cover. It occupies a relatively small geographic area during summer (Mosnier et al., 2010) and is considered a relic from the last glaciation, reproductively isolated from the nearest Arctic and sub-Arctic populations (De March et al., 2002). Severely depleted by commercial hunting, this population declined from 5000 to 10,000 individuals at the end of the 1800s (Reeves and Mitchell, 1984; Hammill et al., 2007) to 1000 individuals or less in 1979 when it was afforded protection (Anonymous, 1979; Lesage and Kingsley, 1998; Hammill et al., 2007). Concern over its future was a determining factor leading to the establishment of a marine conservation park in 1998. The SLE beluga population is currently listed as “threatened” under Canada’s “Species at Risk Act” (DFO, 2012).

Despite the application of protective measures, the SLE beluga has shown no signs of increase over the period 1988–2006 (Hammill et al., 2007) and was estimated at around 1100 individuals in 2007 (Hammill et al., 2007). This apparent failure to recover has generally been ascribed to the impact of anthropogenic activities (Kingsley, 2002), and in particular the presence of high levels of various persistent contaminants in beluga and their environment (Béland et al., 1993; Lebeuf et al., 2014). Two programs are in place to monitor the status of this population: a photographic aerial survey program and a carcass monitoring program.

The photographic survey program has operated since 1988. In addition to abundance indices, these surveys provide information on recruitment through the detection of smaller individuals on the photographs, which can be used as an index of calf production. The surveys provide extensive synoptic coverage of the population’s summer range (49.5%), but remain characterized by large confidence intervals. This high variance is due in part to the correction for the availability bias (i.e. animals underwater when the aircraft passed overhead), but mostly to the high degree of clumping of beluga groups across their spatial distribution which generates large variability in encounter rates among transect lines. A low population size estimate obtained from an aerial survey conducted in 2009 (676 [CI 499–915]; Gosselin et al., 2014) raised concerns that the population could be in decline.

The carcass monitoring program has been in operation since 1983. In addition to tissues collection for various research projects (e.g. pathology, infectious agents, toxicology), animals found dead are measured, the sex is recorded and a tooth is extracted for age determination, thus providing the age structure of this sample of dead animals. Some animals are also examined at necropsy to determine their cause of death. The number of death reports cannot, however, be interpreted as a direct index of mortality rates in the population, because they could also reflect variations in population size or in the probability that carcasses are found in a given year. Moreover, while the carcass monitoring program has been advertised by a publicity campaign each spring with the aim of maintaining constant detection effort, seasonal and annual variations are likely to exist. The carcass monitoring program has highlighted elevated mortalities in 2008, 2010 and 2012, with reports of dead calves three to five times higher than previous maxima (Lesage et al., 2014), which could imply recent changes in population structure and age-specific mortality.

Both the carcass monitoring and survey programs suggest that important changes in the dynamics of this population have occurred, but neither dataset on its own is able to shed light on the internal processes involved. We developed an IPM to integrate the best-available information: (1) population size estimated from seven photographic aerial surveys flown between 1990 and 2009, (2) proportion of young obtained from the same surveys, (3) age and sex composition of dead beluga documented by the carcass monitoring program during the 1983–2012 period, (4) prior knowledge of beluga life-history parameters (e.g. calving rate), (5) catch history for the period 1913–1960. Our objective was to identify mechanisms that best explained recently observed changes.

2. Data and modelling

2.1. Modelling approach

In population dynamics studies, integrated analysis involves fitting a single model to data from multiple sources (Besbeas et al., 2002), such as independent surveys estimating population size and studies designed to obtain population dynamic parameters. This integration is achieved by measuring relative model fit to each data set in a common currency, the likelihood, and then combining them to obtain a global measure of fit. The objective is then to maximise this value (Goodman, 2004; Hoyle and Maunder, 2004). We described changes in population size and parameters with two linked components: the state and the observation processes (State–space models: De Valpine and Hastings, 2002; Buckland et al., 2004). The state process describes the true, but unknown, population dynamics of the SLE beluga population, including the size of the population and the value of demographic parameters at different times. The observation process links these parameters to observations from the monitoring programs (e.g. survey estimates). To allow for flexibility, an age-structured hierarchical model was fitted using Markov chain Monte Carlo (MCMC) methods within a Bayesian framework, in which parameters are estimated by updating distributions representing prior knowledge to posterior distributions, based on the observed data. The Bayesian approach allowed us to take into account a large range of uncertainties related to model parameters (Brooks et al., 2004; Maunder, 2004).
2.2. Data

Population size estimates were obtained from seven photographic strip transect surveys flown in late August–early September 1990, 1992, 1995, 1997, 2000, 2003, and 2009 (summarised in Gosselin et al., 2014). These surveys followed a systematic design with parallel transects lying perpendicular to the main axis of the SLE. The region recognised as the summer area of the population (Fig. 1; Mosnier et al., 2010) was flown in a single day. Population estimates were corrected for reader error using methods similar to Stenson et al. (2002). Briefly, sets of photographs were read by two readers, and identified whales were marked on acetates using a wax pencil. The photographs with identified whales were reread, then the acetates from duplicate readings were overlayed and compared. Sightings that did not line up between the two readings were verified and a decision was made by one of us (JFG) as to whether the unique marks represented whales or not. A correction to account for beluga that were undetected due to sun glare on photos was also applied (Kingsley, 1996) and an expansion factor ($f_1 = 2.021$) was used to extrapolate estimated densities to the unsurveyed area between transects. Finally, a multiplying factor based on the dive cycle of SLE beluga ($f_2 = 2.09$) was applied to compensate for animals that were underwater when the aircraft passed overhead (Kingsley and Gauthier, 2002). The error around each abundance estimate was based on the serial differences in encounter rates among transects of each survey (Gosselin et al., 2007). A survey flown in 1988 was not used in the model because of concerns related to the position of the photographic planes and the area effectively photographed during the survey (Gosselin et al., 2014).

For each survey, beluga identified from the photos as individuals swimming alongside a large animal with a body length less than or equal to half the length of the nearest adult were defined as calves (Gosselin et al., 2014) and were assumed to comprise newborn individuals (age 0) and calves that were born the previous year (approx. 1 year-old) (Lesage et al., 2014). The ratio of these young beluga relative to the total number of beluga counted on the photos was used to estimate the proportion of <2 years-old in the population. A potential difference in detection rate between young and adult beluga could result in uncertainty around those estimates. Young animals are smaller and darker and could be less detectable, but they are likely to spend more time near the surface which would make them more detectable. Although no information was available to define this uncertainty, we included an error term around these values in the model (see Section 2.5).

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 out of the study area into the Gulf of St. Lawrence (Fig. 1) 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 beluga carcasses could be missed. It has also been suggested that young beluga are under-represented in such a database due to their lower buoyancy and 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 (see Section 2.5).

The model also incorporated a time series of hunting catches for the period 1913–1960 (Laurin 1982 in Reeves and Mitchell, 1984). These catches were assumed to be known without error.

A series of 28 visual aerial surveys were also flown in 2001, 2003, 2005, 2007, 2008, and 2009. Considering that they cover a more recent and shorter time period than photographic surveys, show a large variability in abundance estimates and, require different corrections for biases related to the proportion of animals diving and the proportion of animals at the surface missed by the observers (analyses in progress), these visual surveys were not integrated in the fitting process. However, they were compared with model outputs to assess the plausibility of the estimated population trajectory in recent years.

2.3. State process: population dynamics

The dynamics of the population were modelled by considering 11 age-classes grouped into four stages (Fig. 2a). 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:

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

and

$$\exp(-Z_{a,t}) = 1 - M_{a,t}$$

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

The first two classes were assigned to the stages “Newborn” and “Yearling” (Fig. 2a) describing, respectively, beluga born during the current year and individuals less than 2 years-old that survived their first year. Both of these stages included individuals that are dependent on their mother. However, there may be large differences in mortality rates between these two stages (Burns and Seaman, 1985, Dodge, 1990), with some cause of death being specific to the newborn class (e.g. peripartum mortality, see Lair et al., 2014); as a result, newborn mortality ($M_1$, Fig. 2a) was treated independently from other mortalities in our model. The mortality for yearlings ($M_2$, Fig. 2a) was considered to be equal to twice the adult mortality (see fourth paragraph of the Section 2.4). If a female taking care of a newborn or a yearling died during a given year, the latter was considered to have also died during the same year.

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 six age classes in order to allow the model to take into account the time lag that can exist between a change in newborn mortality and its effect on productivity as individuals are recruited into the “Mature” portion of the population. Each of these classes had the same mortality rate ($M_3$, Fig. 2a).

The “Mature” stage comprised individuals 8 years and older that can reproduce (Robeck et al., 2005; Suydam, 2009; 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. Given that mortality rates for “immature” age classes are generally not different from the “Mature” ones (Burns and Seaman, 1985), their mortality rate was considered equal ($M_3$, Fig. 2a).

The beluga reproductive cycle was 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 were assumed not to be 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) that were not pregnant nor with a calf less than 1 year old at the time of reproduction. The model also considered that a female that had lost a calf during its first year of life was available for reproduction the following year, i.e. 1 year earlier than normal, allowing for a shorter reproductive cycle as is sometimes observed (one birth every 2 years versus one birth every 3 years; Vladykov, 1944; Kleinenberg et al., 1964; Sergeant, 1973; Burns and Seaman, 1985). The pregnancy rate (Pregnancy, Fig. 2a.) was then applied only to the proportion of mature females that were
available (PropF), i.e. females not pregnant, not with a calf <1 year-old, or that have lost a calf during the previous year).

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

$$N_{t,1} = (N_{8,t-2} + N_{9,t-2} + N_{10,t-2}) \times 0.5 \times \text{PropF}_{t-2} \times \text{Pregnancy}_{t-1} \times (1 - M_{a,t-1})$$

The model was composed of two parts. The “adaptive part” used a deterministic version of the state model to estimate the population size and structure for the period 1913–1982 (Fig. 2b). 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 ($M_{a}$ and $\text{Preg}$, respectively; see below). Thus, all $M_{a,t} = M_{a}$ and all $\text{Preg}_{t} = \text{Preg}$ (Table 1). Because 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:

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

with $C$ the hunting catches for each age $a$ and year $t$. Hunting mortality at age $a$ 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 over a period of nearly 70 years, conditionally to structuring elements such as the hunt and the population parameters estimated in the second part of the model (“fitting part”, see below), in order to minimize sensitivity to the population structure imposed in the starting year of the model (i.e. 1912).

The “fitting part” used a stochastic version of the state model for the period 1983–2012 (Fig. 2c). Mortality and pregnancy rates were random variables that could vary each year, as would be expected in a wild population. Data acquired through aerial surveys and the carcass monitoring program were used to inform the model during the period 1983–2012 and thus update the priors. The median values of each parameter ($M_{ab}$, $M_{y}$, $M_{adult}$, Pregnancy; Fig. 2c) estimated for 1983–2012 were used as fixed values in the “adaptive part”. Hunting mortality was assumed to be nil during this period.

2.4. Initial state and priors for process parameters

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), which was hunted but was considered to be stable. Therefore, we assumed that the SLE beluga population had a similar stable age distribution at the start of intensive hunting late in the 19th century. 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) instead of one as currently recognised (Stewart et al., 2006; Luque et al., 2007). A multiplicative term, $\alpha$, estimated by the model, was applied to this age structure vector to control for the size of the initial population.

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 $r_{\text{max}} = 1.04$. 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 ($M_{ab}$, Fig. 2c) was given a prior following a Beta distribution with the first parameter ($\alpha$) arbitrarily fixed to 2, and the second parameter ($\beta$) 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 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 two and not one GLG per annum. In the model, we assumed that mortality of yearlings (M1, Fig. 2c) was equal to twice that of adult mortality (Madult, see below).

Mortality rates of older beluga estimated by Burns and Seaman, (1985: 7%), Doidge, (1990: 8.4%) and Luque and Ferguson (2010: 3–8%) 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). We assumed that the mortality rate (Madult) applied to these older beluga, i.e. “immature” and “Mature” stages, followed a Beta distribution, where the first parameter (α) was arbitrarily fixed to 2, and the second (β) was sampled from a Gamma (30, 1) distribution. This resulted in a Beta distribution with a median at 5.4%, and quartiles at 3.1 and 8.7%.

Not all available mature females reproduce each year. Five to 34% of the mature females can be resting, i.e. non-pregnant and non-lactating (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. 2c) 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.

2.5. Observation process: fitting to data

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

\[
\ln(S_t) = \ln(N_t) + \varepsilon_t
\]
with $S_t$ the survey abundance estimate in year $t$, $N_t$ the true population size and $\varepsilon_S$, 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 occurred. These mortalities were thus applied to 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:

$$\ln \left( \hat{P}_S \right) = \ln \left( \hat{P}_N \right) + \varepsilon_{P_S}$$

with $\hat{P}_S$, the proportion of young estimated in the survey, $\hat{P}_N$, the true proportion of young in the population and $\varepsilon_{P_S}$ 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 $\varepsilon_{P_S}$ was given a log-normal distribution with a zero location parameter and a precision ($1/\sqrt{sd}$) sampled from an arbitrary prior taking the form of a Gamma ($20, 1$) distribution. This resulted in a median CV of 23% around $\hat{P}_S$ with quartiles of 21 and 25%.

The number of beluga found dead each year (CarcassFound) 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 (dead), and the probability that these animals were found (pObs). Relationships for newborns and older individuals (i.e. excluding newborns) were described for each year $t$ as:

CarcassFound_{newborn} ~ Bin(pObs_{newborn}, dead_{newborn}) for newborn

CarcassFound_{older} ~ Bin(pObs_{older}, dead_{older}) for older individuals

with $p_{Obs_{newborn}} ~ Beta(\alpha_{nb} \times \varphi_{nb}, \beta_{nb} \times \psi_{nb})$

and $p_{Obs_{older}} ~ Beta(\alpha_{old} \times \varphi_{old}, \beta_{old} \times \psi_{old})$

where $\alpha_{nb} \sim \text{Uniform (0, 1)}$, and $\alpha_{old} \sim \text{Uniform (0, 1)}$

$\beta_{nb} \sim (1 - \alpha_{nb})$

$\beta_{old} \sim (1 - \alpha_{old})$

Factors such as weather conditions (i.e. affecting human presence on shores) could have influenced the effort and thus the detection probability of beluga carcasses (DFO, 2007), but there was no information to help define the values for the probability of finding dead beluga. Therefore, $p_{Obs_{newborn}}$ and $p_{Obs_{older}}$ were sampled from Beta distributions with mean values ($\alpha_{nb}, \alpha_{old}$) themselves sampled from non-informative Uniform distributions bounded between 0 and 1. The error around the mean was controlled by a multiplying factor $\varphi$. We defined the value of $\psi_{nb}$ and $\psi_{old}$ as 100 and 300, respectively, assuming potential mean values for $p_{Obs_{newborn}}$ and $p_{Obs_{older}}$ of 0.07 and 0.26. It resulted in quartiles of 0.052, 0.086 for $p_{Obs_{newborn}}$ and 0.242, 0.277 for $p_{Obs_{older}}$.

### 2.6. 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 using packages R2jags and coda developed in the R programming language (R Core Team, 2013). Each model run included three 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).

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 ($\alpha_{nb}$ and $\alpha_{old}$ for carcasses detection, Npop_{1988} as the abundance estimate obtained 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 also tested.

Sensitivity of the results to the initial population structure was tested using two alternative age structures. The first was obtained from a Leslie matrix using population parameters based on the
Fig. 3. Posterior distributions of (a) newborn mortality ($M_{nb}$), (b) adult mortality ($M_{adult}$), (c) pregnancy rate of the females available for the reproduction (Pregnancy), (d) pregnancy rate considering all females occurring in the population (Pregnancy (Pop. Wide)), and (e) probability of detecting carcasses of newborn (pObs Newborn) or (f) older beluga (pObs Older), for each year of the “fitting period” (see section “State process: population dynamics”). Prior distributions are also presented as a reference to identify when information is updated in the model, noting that scales for pObs prior and posterior distributions differ. Median, 50th and 95th percentiles of each distribution are shown as hollow dots, dashed lines and dotted lines, respectively.
carcass monitoring data (following the methodology described in Caughley, 1977; Bélanger et al., 1988). The second test assumed an absence of age structure in giving the same proportion of the population to each age class. Sensitivity of the results to the prior distributions of parameters \( M_{ab} \), \( M_{adult} \). Pregnancy, \( pO_{obsab} \) and \( pO_{obsold} \) 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 photographic 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 full 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.

3. Results

3.1. Estimation of life-history parameters

The model passed all convergence and stationarity tests for the three chains used. Posterior median of newborn mortality (\( M_1 \)) was 23.7% (95% CI 16.5–32.7) and 6.1% (95% CI 5.0–7.2) for the adult mortality (\( M_3 \)). The pregnancy rate of mature females available for reproduction (\( \text{Preg} \)) was 76% (95% CI 64.5–85) and the corresponding proportion of pregnant females in the population was 32.6% (95% CI 27.6–36.9). Cross-correlation tests (Table 2) showed that the model tended to decrease the probability of detecting carcasses of newborns (\( a_{ab} \)) and older individuals (\( a_{old} \)) when it increased newborn mortality (\( M_1 \)) and adult mortality (\( M_3 \)), respectively. An increase in adult mortality (but not in newborn mortality) was strongly correlated with a decrease in the 2012 population size estimate (\( N_{pop2012} \)).

Newborn mortality (\( M_{ab} \)), adult mortality (\( M_{adult} \)), pregnancy rates (\( \text{Pregnancy} \)), and the probability of detecting carcasses of dead newborn (\( pO_{ab} \)) and older beluga (\( pO_{old} \)) 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 3–4 years (Fig. 3a). 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 2 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. 3b). The median of the annual adult mortality was 6.1% but ranged from 4% (1987, 2005) to 8.7% (2004), with high values in the late 1980s early 1990s with two peaks to 7.8% (1989, 1993). Posterior distributions of annual pregnancy rate among available mature females showed relatively stable values at around 80% between 1983 and 1998, becoming unstable afterwards (Fig. 3c). The effect of changes in pregnancy rates was more obvious when considering the posterior distributions of the proportion of pregnant female at the population level (i.e., among all mature females, Fig. 3d). Small peaks in pregnancy were visible every 3 years until the mid-1990s (Fig. 3d). Two higher peaks occurred afterwards in 2000 and 2003, with more than 50% of the females being pregnant, separated by 2 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 (\( pO_{obsab} \), Fig. 3e). Before 2007, the median value of \( pO_{obsab} \) 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 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. 3f) with a median value of 20.2% (95%CI 14.5–27.2%).

3.2. Population trajectory and population structure

The model estimated the SLE beluga population at 1017 individuals (95%CI 866–1200) in 1988 (Fig. 4). 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 model estimated that the population decreased at −1.1% per year to 889 individuals (95%CI 672–1167) in 2012. The model estimate for 2009 (934 individuals with 95%CI 760–1150) was notably higher than the value obtained from the aerial photographic survey flown that year (676 beluga with 95%CI 470–882; Gosselin et al., 2014).

Consistent with the pattern observed in the pregnancy rates (Fig. 3d), the proportion of young beluga (0–1 years old) in the population showed small peaks every 3 years until the mid-90s, remaining at around 13.7% between 1983 and 1998 (Fig. 5a). Thereafter, the proportion of young 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 (Fig. 5a). 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. 5b). 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. These high values were
Table 2
Cross-correlation matrix among posterior distributions of eight selected model variables (M1, M3, Preg, PregPop, \(\alpha_{\text{nb}}\), \(\alpha_{\text{ol}}\), \(\text{Npop}_{1988}\), and \(\text{Npop}_{2012}\)). See Table 1 for a description of variables.

<table>
<thead>
<tr>
<th></th>
<th>M1</th>
<th>M3</th>
<th>Preg</th>
<th>PregPop</th>
<th>(\alpha_{\text{nb}})</th>
<th>(\alpha_{\text{ol}})</th>
<th>(\text{Npop}_{1988})</th>
<th>(\text{Npop}_{2012})</th>
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</thead>
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<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
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<td></td>
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<tr>
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<td>1.00</td>
<td></td>
<td></td>
<td></td>
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</tr>
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<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>&lt;0.01</td>
<td>-0.11</td>
<td>-0.11</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(\alpha_{\text{ol}})</td>
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<td>-0.07</td>
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<td>1.00</td>
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<td></td>
</tr>
<tr>
<td>(\text{Npop}_{1988})</td>
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<td>&lt;0.01</td>
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<td>-0.76</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
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<td>-0.70</td>
<td>0.03</td>
<td>0.03</td>
<td>-0.04</td>
<td>0.29</td>
<td>-0.07</td>
<td>1.00</td>
</tr>
</tbody>
</table>

associated for the most part with a higher pregnancy rate in the previous year (Fig. 3d) and a higher newborn mortality (Fig. 3a). Only in 2012 did the model also suggest that the large number of newborn carcasses found was in part explained by an increase in the probability of detection (Fig. 3e).

Model estimates of the number of deaths among beluga aged 1-year and older, i.e. yearlings, immature and mature age classes, were consistent with observations from the carcass monitoring program (Fig. 5c). Results did not indicate a trend in the number of deaths but exhibited 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 per annum.

The evolution of the age structure (Fig. 6), from a stable state before 2000 to a highly disturbed distribution afterward, highlights the consequences of the important changes in productivity and newborn mortality that occurred between 1999 and 2006 (Fig. 3a, c and d). One particular gap, visible in 2006 (Fig. 6), was created between the two peaks of production in 2001 and 2004 (see appendix Fig. A.1 for propagation of that gap through the population). The model estimated that the proportion of mature individuals in the population increased starting in 1999 (Fig. 7b). However, this increase did not result from an increase in the number of mature individuals which remained stable, but from the decrease in the number of immature beluga. The model also estimated a decrease in the proportion of newborns in the population from 6–8% before 1999 to 4–6% after 2007 (Fig. 7a).

3.3. Model diagnostics and sensitivity

The choice of the initial population structure did not affect model parameter estimates (Fig. 8, Fig. A.1), demonstrating the usefulness of the adaptive part of the model and the robustness of the final age structure. Estimated newborn mortality was sensitive to the choice of its own prior distribution, but the model compensated for higher newborn mortality by increasing pregnancy rates and reducing the probability of detecting newborn carcasses, which had a limited effect on the 1988 and 2012 population size estimates. The model was more sensitive to the prior for adult mortality: using extreme prior values (median 15.2%) resulted in a posterior median mortality of 7.6% and a low 2012 population size (600 beluga), with a population declining continuously since 1913. Conversely, lower prior values resulted in continual growth from the end of the 1950s to the present and a poor fit to survey estimates.

Pregnancy rate posteriors were sensitive to their prior distribution, but the effect on the population size estimates was limited, even for the two extreme cases tested (e.g. median values in 2012 of 854 and 698, vs. 889 beluga for the main model). Lower priors for fecundity were compensated for the most part by a decrease in adult mortality. Modifications of the value of \(\varphi_{\text{nb}}\) and \(\varphi_{\text{ol}}\) respectively, controlling the variance of \(p_{\text{Obsnb}}\) and \(p_{\text{Obsol}}\), had only a small effect on the results (Fig. 9, Appendix Table A.1).
When fitted exclusively to aerial survey abundance estimates, the model estimated a slightly higher population size in 1988 and a lower population size in 2012 (776 vs 889 beluga for the reference run), with a steeper overall decline (Fig. 9). This difference was associated with a slightly higher newborn and adult mortality (Fig. 8). When using both survey abundance estimates and the proportion of young detected on aerial photos, and leaving carcass data out, population trajectory varied more widely among years (Fig. 9) as changes in age structure, newborn mortality and pregnancy rate were necessary for the model to fit changes in observed proportion of young.

Incorporating the newborn carcass dataset decreased newborn and adult mortality rates to values below those of the reference run (Fig. 8), and informed the model on year-to-year variations in pregnancy rates. Together with variability in newborn mortality, these variations explained the recently observed peaks in newborn death reports. This affected the overall population trajectory, which was estimated to first increase before decreasing due to lower recruitment (Fig. 9). Finally, integrating the carcass data for older beluga reduced the variability in adult mortality rates and had a stabilizing effect on the population trajectory as a result of the number of non-newborn carcasses being largely stable over time. This 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 (Fig. 9).

Fig. 6. Evolution of the St. Lawrence Estuary beluga population age structure estimated by the population dynamic model for the period 1988–2012. Only five representative years are presented (i.e. 1988, 1994, 2000, 2006, 2012). The complete annual evolution is available in appendix (Fig. A.1). Note: The proportion of immature animals indicated in this figure included individuals <8 years old.

Fig. 7. Model estimates of the proportion of the St. Lawrence Estuary beluga population (black line with open circles) represented by (a) newborn, (b) mature individuals (≥ 8 years old) over the period 1983–2012. The dashed line shows the corresponding number of mature individuals over the same period. See appendix (Fig. A.1) for the evolution of proportion of each age class.
Fig. 8. Sensitivity of the median estimates (solid black circles) 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 and appendix (Table A.1) for detailed values.

Removing the 2009 abundance estimate from the fitting process changed the estimated population trajectory, with the population increasing since the 1950s as a result of a lower estimated adult mortality, then stabilizing around 1200 beluga over the last 6–8 years of the modelling period (Fig. 8). As in the main model, the change in population trajectory in later years was due to changes in age structure and population dynamic parameters starting around 1999.

4. Discussion
4.1. Population trajectory and structure

Our integrated population model combining information from multiple sources (aerial surveys, carcass monitoring program, catch history) into a single framework, along with a detailed representation of the age structure and life-history parameters of the SLE beluga, yielded a plausible population trajectory leading to the recently observed changes. 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 the year 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 the population has declined in recent years.

The model also suggested that internal changes in population dynamics and age-structure have occurred along with this decline.
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. 3a) and stable pregnancy rates (around 30%, with small peaks every 3 years, Fig. 3d). During this period, population age structure was stable with the ratio of mature to immature close to 58:42 (considering immature as 0–7 years old beluga), and the proportion of newborns around 7.5%.

In contrast, the period 1999–2012 was characterized by demographic instability and wide 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, 2007, 2009, 2011), the latter separated by periods of lower-than-average pregnancy (e.g. ~15% in 2001–2002).

A particularly striking pattern emerged over the last 6 years of the modelling period, with female reproduction estimated to have changed from a 3-year cycle (with a third of mature females pregnant each year; before 1999 on Fig. 3d) to a 2-year cycle (with about half of the females pregnant each year; 2006–2012 on Fig. 3d). This pattern was concurrent with a highly variable newborn mortality while following an increasing trend (2006–2012 on Fig. 3d). These drastic changes in reproduction dynamics had strong cascading effects on the population age structure (Figs. 6 and 7). As a consequence, the proportion of newborns in the population 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, resulting in a ratio of mature to immature of 67:33 by 2012. However, their absolute numbers stayed constant.

### 4.2. Uncertainty and sensitivity

The strength of this model was its ability to incorporate data from multiple sources, thus providing more information for inference. Both empirical (Besbeas et al., 2003) and simulation studies (Abadi et al., 2010) have shown that integrated population models deliver demographic estimates with a higher precision than separate conventional models. Because each of the 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. Similarly, cross-correlation among some parameters (e.g. newborn mortality and the probability of detecting carcasses) suggests that the model does not always have enough information to distinguish among possible scenarios (e.g. less newborn deaths in a given year versus less efficient detection of carcasses), thus increasing reliance on priors. 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 attributed the decline in abundance to 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 carcass monitoring data were essential for the model to find a mechanism for the decline in abundance. However, they also made it more difficult 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 for little variation of population size across the period, apparently in contradiction with results from the latest survey. The model explained this by suggesting that the population decline was due to lower recruitment, but that absolute numbers of adults were stable over the same period, thus keeping the number of adult carcasses relatively constant. Although carcass data may have a disproportionate weight in model fitting because these data are collected on an annual basis, whereas the surveys are only flown every 3–5 years, sensitivity tests showed that the 2009 abundance estimate had an important effect on model predictions, demonstrating that both carcass and survey data inform posterior distributions. Interestingly, even without the 2009 survey, the model still identified similar changes in age structure and population parameters around the year 1999.

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; Heide-Jørgensen and Teilmann, 1994). Moreover, small regular peaks in pregnancy suggest some degree of synchrony among females in part of the population. Such synchrony had already been proposed by Kingsley and Hammill (1991) as an explanation for the change in the proportion of young observed between the 1988 and 1990 aerial surveys. While the 1988 survey results were not used to fit the model, our results did suggest a low proportion of young in 1988 and a high value in 1990, which matched survey estimations.

Additionally, a long-term photo-identification program of live SLE beluga (1989–2012) indicated changes in age structure and
4.3. 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 confirms 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 episodes of high newborn mortality. Initially, these mortalities were not reflected in survey estimates, likely because, as is observed in other long-lived species (Goodman, 1981; Gaillard and Yoccoz, 2003), the age structure of the beluga population prevented short-term variations in abundance in response to pulsatile 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 the following year, rather than following the normal 3-year cycle, resulting in years with over half of the mature females being pregnant at the same time. These peaks of pregnant females were usually followed the next year by a peak in the rate of newborn mortality, i.e. an increase in newborn deaths that was disproportional to the increase in births, suggesting environmental or intrinsic limits to these excessive birth rates. This would in turn free more females for reproduction in the following year, creating the appropriate conditions for repetition of this cycle.

The overall decrease in numbers of beluga observed in recent surveys (Gosselin et al., 2014) thus 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 6 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; Scarratt et al., 2014; Starr et al., Unpublished results). 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.

Median adult mortality was estimated by the model at 6.1%. Although this value falls within the 3–8% range estimated by Luque and Ferguson (2010) for five hunted populations of beluga, one would expect a lower adult mortality rate for SLE beluga, which has been protected from hunting since 1979. However, the SLE beluga population is at the southern limit of the species distribution and lives in an environment that has been severely perturbed over the last 100 years. Following significant depletion during a period of intense hunting, it now faces many other threats, including high contaminant loads, recurrent toxic algal blooms, environmental degradation due to fisheries activities and climate variability, and chronic exposure to high levels of marine traffic (McQuinn et al., 2011; Gervaise et al., 2012; Lebeuf et al., 2014; Plourde et al., 2014; Starr et al., Unpublished results) in addition to the potential effect of inbreeding caused by their small population size (Patenaude et al., 1994). These elements, acting separately or in combination, could account for high mortality rates and the lack of recovery of this population. Additional work is needed to determine if any recent changes in the environmental factors identified above could have resulted in the changes observed in population dynamics since 1999.

Integrated population models are flexible tools that can be adapted to a variety of sampling situations (Schaub et al., 2007). Conservation of the SLE beluga relies on two long-term monitoring programs. Separately, neither dataset could confirm population decline or explain the internal processes involved. By combining independent sources of data in a single integrated model, we were able to estimate population size and demographic parameters with increased precision. Another advantage of this framework is that it allowed us to model biologically plausible population processes by including realistic behaviour (females becoming available for reproduction following calf death), and it had the required flexibility to fit to annual and multi-annual data. These characteristics of our modelling approach were all necessary to propose proximal mechanisms working at fine temporal scales that could be responsible for the observed changes in population structure. Prospective analyses should link results of our integrated population model with environmental parameters in order to improve our understanding of events that may have contributed to the recent decline of the SLE beluga population.

Acknowledgements

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Appendix A.

Fig. A.1 Table A.1
Table A.1
Output values (median and 95%CI), for eight variables of interest (M1, M3, Preg, PregPop, αad, αald, Npop2009, 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 Fig. 8.

<table>
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<tr>
<th>Variables</th>
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<td>50%</td>
<td>97.5%</td>
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</tr>
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<tr>
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<tr>
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<td>0.255</td>
</tr>
<tr>
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</tr>
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<td>0.218</td>
<td>0.298</td>
</tr>
<tr>
<td>pObs αald</td>
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<td>0.331</td>
</tr>
<tr>
<td>pObs ϕad</td>
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<td>0.250</td>
<td>0.344</td>
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<td>0.218</td>
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</tr>
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<td>Madult beta(2, gamma(50,1))</td>
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<td>0.233</td>
<td>0.322</td>
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<td>Preg beta(gamma(4,1), gamma(20,5))</td>
<td>0.482 (50%CI 0.319 – 0.637)</td>
<td>0.161</td>
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<td>0.314</td>
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<td>pObs ϕad 30 and pObs ϕad 100</td>
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<td>0.176</td>
<td>0.333</td>
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<td>0.229</td>
<td>0.318</td>
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<td>0.172</td>
<td>0.245</td>
<td>0.330</td>
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<tr>
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<td>0.164</td>
<td>0.234</td>
<td>0.323</td>
<td>0.041</td>
</tr>
<tr>
<td>Without 2009 abundance estimates</td>
<td>0.164</td>
<td>0.234</td>
<td>0.321</td>
<td>0.042</td>
</tr>
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<td><strong>Init Pop.</strong></td>
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<tr>
<td>(M_{\text{ini}})</td>
<td>0.239</td>
<td>(50% CI 0.138 – 0.375)</td>
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<tr>
<td>(M_{\text{ini}})</td>
<td>0.054</td>
<td>(50% CI 0.031 – 0.087)</td>
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<tr>
<td><strong>Burns and Seaman (1985)</strong></td>
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<td><strong>Priors</strong></td>
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<tr>
<td>Leslie Matrix</td>
<td>0.041</td>
<td>0.063</td>
<td>0.092</td>
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<tr>
<td>AllTheSameProp</td>
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<td>0.063</td>
<td>0.093</td>
<td>NA</td>
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<tr>
<td>Without 2009 abundance estimate</td>
<td>0.039</td>
<td>0.059</td>
<td>0.088</td>
<td>0.169</td>
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</table>
Fig. A.1. 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 section “State process: population dynamics”) over the period 1983–2012. The last graph shows the proportion (black line and hollow dots) and the number of individuals (grey dotted line) considered mature (8 years old and older).

References