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Historical abundance of Eastern Canada - West Greenland (EC-WG) bowhead whales (*Balaena mysticetus*) estimated using catch data in a deterministic discrete-time logistic population model

Jeff W. Higdon[1] and Steven H. Ferguson[2]

[1]Higdon Wildlife Consulting
912 Ashburn Street
Winnipeg, MB R3G 3C9

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

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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.

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ABSTRACT

Applying a Precautionary Approach to marine mammal harvesting requires knowledge of abundance trends, population dynamics, and carrying capacity of the target species. We use historical catch data to model bowhead whale (*Balaena mysticetus*) population abundance trends over the past 500 years. The analysis provides an estimate of the historic (i.e., pre-exploitation) population level that can be used as a carrying capacity (K) estimate in identifying limit reference points in management. A standard discrete time logistic growth model used by the International Whaling Commission to understand past and future population abundance projections was developed for the Eastern Canada-West Greenland bowhead population. A number of model runs investigated parameter estimation and sensitivity and provided confidence in the approach. The model results provided an historical population size estimate of about 18,500 whales as the most plausible solution (mean = 18,495; 95% CI = 18,022-18,972; SD = 289 for a model with input K = 18,000-19,000 and with mean r_{max} = 0.0400; SD = 0.0029; 95% CI = 0.0352-0.0448). A rough estimate of a historic population size of 18,500 and a current population estimate of 10,000 would indicate that the population is currently at ca. 54% of K.

Abondance historique des baleines boréales (*Balaena mysticetus*) de l'est du Canada et de l'ouest du Groenland, estimée à partir des données sur les prises selon un modèle logistique déterministe de population en temps discret

RÉSUMÉ

Pour appliquer une approche de précaution à la chasse des mammifères marins, il faut connaître la capacité biotique, la dynamique des populations et les tendances relatives à l'abondance des espèces ciblées. Pour modéliser les tendances relatives à l'abondance des populations de baleines boréales (*Balaena mysticetus*) au cours des 500 dernières années, nous avons eu recours aux données historiques sur les prises. L'analyse réalisée permet d'estimer le niveau de population historique (c.-à-d. avant exploitation), lequel peut servir d'estimation de la capacité biotique (K) aux fins de l'établissement de points de référence limite pour la gestion des ressources visées. Un modèle logistique standard de croissance en temps discret utilisé par la Commission baleinière internationale pour comprendre les projections de l'abondance passée et future des populations a été développé pour la population de baleines boréales de l'est du Canada et de l'ouest du Groenland. Plusieurs exécutions du modèle ont permis de sonder l'estimation et la sensibilité des paramètres et de garantir la pertinence de la méthode. Selon les résultats obtenus à l'aide du modèle, l'estimation la plus plausible de l'effectif historique de la population est d'environ 18 500 baleines (moyenne = 18 495; intervalle de confiance à 95 % = 18 022-18 972; écart type = 289 pour un modèle avec où K = 18 000-19 000 et un taux d'accroissement maximum du stock [Rmax] moyen = 0,0400; écart type = 0,0029; intervalle de confiance à 95 % = 0,0352-0,0448). Sachant que la population actuelle est estimée à 10 000 individus, l'estimation approximative de l'effectif de la population historique à 18 500 animaux indique que la population est aujourd'hui à 54 % environ de sa capacité biotique K.

INTRODUCTION

DFO adopted a Precautionary Approach (PA) to establishing harvest levels for marine mammals in Canada (Stenson et al. 2012), which attempts to use a level of caution proportional to the level of stock assessment knowledge. The PA model does not consider the absence of information to be a reason for not implementing conservation measures, and defines decision rules in advance for management when the stock in question reaches clearly-stated reference points (Punt and Smith 2001). These reference points (or levels) are referred to as limit, precautionary, and target reference points (ICES 2001; DFO 2009). The identification of critical (N_{lim}) and precautionary (N_{buf}) levels creates three zones: a 'critical zone', a 'cautious zone', and a 'healthy zone'.

The amount of information available for harvest management varies among populations, and DFO distinguishes two broad categories: "data rich" and "data poor" (Stenson et al. 2012). Data-rich populations are those for which managers and biologists think there exists a reasonable understanding of their recent abundance and population dynamics. Currently, data-rich species are defined by DFO as having three or more abundance estimates over a 15-year period, with the last estimate obtained within the last five years, and current information (within the last five years) on fecundity and/or mortality to determine sustainable levels of exploitation. Initial definitions of the level of stock knowledge required to use data-rich methods were derived for Northwest Atlantic seals (Hammill and Stenson 2007). However, due to their large size and slow demography, whales are expected to require modified definitions (Stenson et al. 2012). If population trend and demographic data are not available, the species would be considered as data-poor and managed using the more conservative Potential Biological Removal (PBR) approach (Wade 1998).

Bowhead whales (*Balaena mysticetus*) in the Eastern Canada-West Greenland (EC-WG) stock are currently managed as data poor using the PBR method. However, the potential exists to manage this stock as data rich given recent survey efforts (Doniol-Valcroze et al. 2015) and knowledge of species life-history traits (Nerini et al. 1984). To use a model-based approach for a data rich species requires an estimate of historic abundance to assist in setting reference points. Bowhead whales were commercially harvested in eastern Canadian and West Greenland waters for over 500 years (Higdon 2008, 2010). As a result of overharvest, the population was reduced to extremely low numbers and considered commercially extinct by the early 1900s (Ross 1979, 1993). The population has since shown some level of recovery; however, it is unknown to what extent populations have recovered to pre-exploitation numbers. We used a bowhead whale catch history (Higdon 2010) and a deterministic population growth model to estimate the historic (pre-exploitation) population size of the EC-WG bowhead whale stock.

METHODS AND RESULTS

The harvest series compiled by Higdon (2008, 2010) is used here to conduct deterministic modelling of bowhead whale population trajectories over time. We use a discrete-time logistic growth population model with uniform distributions for parameter ranges to estimate the size of the bowhead whale population prior to commercial whaling. The model was run multiple times, with continued refinement of parameter ranges (based on available empirical data) until we arrived at a solution (i.e., estimate of carrying capacity, K) that was deemed reasonable based on the resulting population trajectory and its status in the early 1900s (commercial extinction) and at present (compared to recent abundance estimates). These results can be used to set limit reference points (LRPs) for management of the EC-WG bowhead whale population, or to establish plausible parameter ranges for more detailed modelling.

POPULATION MODEL

The model is a standard discrete time logistic growth model as used by the International Whaling Commission (IWC), a variant of the standard Pella-Tomlinson model, with no modelling of the Allee Effect. The model projects forward and is defined as:

$$P_{t+1} = P_t + r_{max}*P_t\ (1 - (P_t\ /K)^z) - (C_t*\Omega) \qquad [1]$$

where P_t is total population size during year t, r_{max} is the intrinsic rate of increase, K is carrying capacity, assumed to be equal to abundance before exploitation (i.e., $P_{t=0}$), z is the exponent setting the maximum sustainable yield level (MSYL); that is, the size of the population, relative to K, at which the maximum number of whales can be taken without changing the population size (e.g., 2.39 when MSYL is 60% of K, as conventionally assumed for whales), C_t is the recorded catch in terms of numbers of whales during year t, and Ω is a correction for whales killed and lost (or struck and lost that subsequently died from their injuries).

DATA AND PARAMETER VALUES

The model requires time series data on bowhead catches, and parameter values for carrying capacity (K) (assumed to equal the initial population size prior to exploitation), population growth rate (r_{max}), the exponent setting the MSYL (z), and killed but lost rates (Ω). The exponent setting the maximum sustainable yield level (z), i.e., the shaping parameter, is 2.39 when MSYL is 60% of K, which is conventionally assumed for large whales. This value was used for all model runs, as there are no empirical data on its true value (Whitehead 2002) (also see Witting 2011). Some preliminary (fully-deterministic) modelling was conducted using three different values for z (1.00, 2.39 and 5.00; Witting 2011) to explore the effect on model behaviour. Higher z-values resulted in larger population nadirs (i.e., populations that were less depleted) and faster recovery. Some population trajectories that went extinct with z = 1.00 and/or 2.39 were fully recovered with z = 5.00 (e.g., K = 15,000 and Ω = 1.10).

Three variables are unknown, including the primary variable of interest, K (carrying capacity), assumed equal to the pristine population size. The other two unknown parameters are the population growth rate, r_{max}, and the correction factor for whales that were killed but lost (Ω). There are however some empirical data for these parameters.

Harvest series

The commercial whaling catch series in Higdon (2010) runs from 1530 (estimated start of Basque whaling in the Strait of Belle Isle) to 2009 (Figure 1). Inuit subsistence harvests are estimated extending back to 1200 AD, the approximate arrival of Thule people to the Canadian central and eastern Arctic. Harvests were not corrected for struck and lost, with the exception of recent (post-commercial era) Inuit harvests where these data are available. The harvest series was updated with recent catches (2010-2011) from DFO (unpublished data) and Greenland (Heide-Jørgensen et al. 2012). More recent catches (2012-2014) are available for Canadian subsistence harvests (n = 8 whales, 2-3/year), but recent Greenland harvests have not been reported to the IWC. The cumulative reported catch from 1500 (model was started in 1499) to 2011 is 70,947 whales (Figure 1).

Population growth rate

Population growth rate of the EC-WG bowhead whale population is not known. In the Bering-Chukchi-Beaufort (BCB) population, growth has been estimated as 3.4%, with upper and lower 95% confidence intervals of 1.4% and 5.1% (George et al. 2004). The authors noted however that the population was not growing at its maximum possible rate. A more recent estimate of 3.7% has been endorsed by the IWC (2013, confidence intervals not stated). Wade (1998) used 0.04 as a theoretical maximum population growth rate for cetaceans.

Correction for killed but lost whales

Previous bowhead modelling exercises have used killed/lost rates of 15-20%. For the Spitsbergen stock, Mitchell (1977) applied a loss rate of 20%, based on a 15% loss rate estimated from logbooks for 1791-1822 and increased by 5% because he assumed the earlier fishery (during the decade of peak harvests) to be less efficient. Mitchell and Reeves (1981) used a loss rate of 15% from the 1792-1822 Spitsbergen fishery in their calculation for the Davis Strait "stock", and Mitchell (1977) (also see Reeves and Mitchell 1990) used a loss rate of 20% (as used for the early Spitsbergen fishery) in calculating the pristine size of the Hudson Bay "stock". Woodby and Bodkin (1993) used the same values for their population growth models of the two putative stocks. Mitchell (1977) estimated struck/lost corrections of 24% for the Bering-Chukchi-Beaufort (B-C-B) stock, using data from logbooks and other historical records.

Higdon (2008, 2010) suggested that corrections of 15-20% might be too low, at least for some whaling eras, based on occasional reports of higher losses. Reeves and Cosens (2003) examined logs covering 50 American whaling voyages to Hudson Bay (92 ship-seasons as vessels would often overwinter). Their database (provided by the authors, also see Higdon and Ferguson 2010) includes strikes of 353 bowhead whales, of which 307 (87%) were killed and secured. Only five whales (1.4%) were killed and lost, and 41 (11.6%) were struck and lost. Not all of those whales struck and lost would have suffered fatal wounds, and many would have survived. These harvests are from Hudson Bay only, but unpublished data from Baffin Bay and Davis Strait (R.R. Reeves, pers. comm., D.B. Stewart, pers. comm.) shows similar trends. Analyses of available logbooks therefore suggests that corrections of 15-20% are reasonable.

INITIAL MODEL RUNS

The model was first run in a fully-deterministic manner, using a combination of parameter values. Model runs used K values ranging from 10,000 to 25,000 whales in increments of 5,000 whales and r_{max} values of 0.030 to 0.050 in 0.05 increments. Corrections for killed and lost whales (Ω) ranged from 10 to 20% in 5% increments. It was not necessary to examine all possible variable combinations. For example, if a population size K goes extinct under the most relaxed growth and loss scenarios, there was no need to examine the same population with lower growth rates and higher loss corrections. Results from these fully-deterministic were used to guide selection of reasonable parameter value ranges for simulation modelling.

Selected results from these model runs are summarized in Table 1. Any scenario with a starting population (K) of 10,000 or 15,000 goes extinct, even with minimal killed/lost correction (Ω = 0.10) and maximum population growth rate (r_{max} = 0.050). A scenario with K = 20,000 goes extinct with a low r_{max} (0.030) and high Ω (0.20), but survives and is fully recovered if Ω is lower (0.10). Overall, these results would suggest that the initial model set, using empirically-supported Ω values from 0.10 to 0.20 and r_{max} values of 0.30 to 0.50, should explore K values ranging from 15,000 (which will result in extinction) to 20,000 (which will range from extinction to full recovery, depending on the parameter values for r_{max} and Ω). The initial model set therefore used these parameter ranges, set up with uniform distributions.

SIMULATION MODELLING

All simulation models were done using the Pop Tools add-in for Excel. Population trajectories were modelled using the Monte Carlo simulation tool. The initial model runs used uniform distributions for parameter values for K (15,000-20,000), r_{max} (0.030 to 0.050), and Ω (1.10-1.20). The model was started in 1499 (i.e., year = K), with 30 years of Inuit subsistence harvests (estimated by Higdon 2010 as 31/year) prior to the initiation of Basque whaling in 1530. The logistic growth model was then run for 10,000 simulations. For each run we extracted parameter values for K, r_{max}, and Ω, in addition to the resulting population estimate for each year (P_{1500} to P_{2011}). The first model was run with wider variable ranges to examine general model behaviour and explore relationships between parameters, and was subsequently refined based on the results of the first simulation set and available empirical evidence (i.e., for r_{max} and Ω).

Correlations were used to assess model behaviour. Correlations (lack thereof) between variable pairs (i.e., K and r_{max}, K and Ω) were used to confirm that parameters were drawn at random for each run, and autocorrelation at lags 1 and 2 was used to determine if each successive iteration was independent.

ESTABLISHING PLAUSIBLE POPULATION TRAJECTORIES

Several lines of reasoning were used to determine whether mean population trajectories were plausible given the chosen parameter ranges (K, r_{max}, Ω): a) the nadir (minimum) population size, and b) the population size in 2011. We used 2011 as the cut-off as this was the last year that Greenland harvests have been reported. We defined a recovered population as one that is at 70% of K or higher at the end of the trajectory (see Stenson et al. 2012), and defined a fully recovered population as one that is at 90% of K or higher at the end of the trajectory.

When commercial whaling ended ca. 1915, bowhead whales were at such low numbers that the population was considered to be commercially extinct (Ross 1979, 1993). The only part of the stock's range that was not visited by commercial whalers was Foxe Basin (Higdon 2010), and this area likely represented a refugia for small numbers of whales. The nadir population size is unknown, but trajectories that never go below a population size in the mid- to high-thousands can clearly be considered unlikely given the known status of the population in the early 1900s. Parameter value combinations that lead to population extinction can similarly be considered implausible.

Recent bowhead whale abundance has been estimated from both aerial surveys and genetic mark-recapture analyses. Koski et al. (2006) analyzed data from March 1981 aerial surveys of the EC-WG winter range and estimated a total population of 1,549 (95% CI 589-4,072). The authors projected a population size of 3,633 (95% CI 1,382-9,550) in 2004, assuming a population growth rate of 3.4% per year (George et al., 2004). Aerial surveys conducted in the 1990s only covered a small portion of the range and do not provide information on total abundance (Cosens et al. 1997; Cosens and Innes 2000; Heide-Jørgensen and Acquarone 2002). More extensive aerial surveys were conducted by DFO in summers 2002 to 2004, but they also did not cover the full extent of the summer range in the eastern Canadian Arctic. These aerial survey data have undergone a number of analyses using different statistical approaches and assumptions, providing a range of population estimates. Abundance estimates from these analyses are presented in Table 2 and range from a minimum of 6,344 (95% CI = 3,119-12,906) (IWC 2009) to a maximum of 14,400 (95% CI = 4,811-43,105) (Dueck et al. 2008). While these estimates are relatively imprecise, they all indicate that the EC-WG population numbered in the mid-thousands in 2002. Since these surveys did not cover the entire summer range, they are considered to be conservative estimates. Table 2 also includes several more recent estimates (see Discussion).

A total of six sets of Monte Carlo model simulations (n = 10,000 runs per set) were run, with parameter values continually revised based on the results of the previous simulation set. The parameter ranges used in the different model sets are summarized in Table 3. Simulation model 1 was run to explore model behaviour and parameter relationships, and is described in detail. It used a wider range for r_{max} than the subsequent models (r_{max} = 0.030-0.050 versus 0.035-0.045). Following this, the other five models all had slightly refined ranges for K, and these models are described as a set.

SIMULATION MODEL 1

The first set of simulation runs (n = 10,000) used K = 15,000-20,000, r_{max} = 0.030-0.050, and Ω = 1.10-1.20 (Table 3).

Model diagnostics indicated no significant ($P > 0.05$) correlations between parameter values for each model run (Table 4). There was also no significant autocorrelation (at lags of 1 or 2) for values of r_{max}, Ω and K (Table 5), so values for each parameter were randomly drawn for each successive iteration.

Population trajectories vary widely with different parameter values, ranging from extinction to full recovery at present (Figure 2). The mean and median values for K were similar, but the median trajectory went extinct whereas the mean trajectory showed a recovery to ca. 6,000 whales in 2011. Over half (n = 6,674) of the 10,000 model iterations resulted in a population that went extinct. A wide range of parameter value combinations for K, r_{max} and Ω resulted in population extinction (Figure 3). Nearly all the remaining trajectories (n = 3,300) recovered (≥ 70% of K), and only 26 fell in between these two extremes.

Correlations between parameter values and the 2011 and nadir population levels reveal which parameters have the largest effect on population trajectories. The values chosen for K and r_{max} both had a large effect on the level of population recovery in 2011 and the maximum level of depletion (measured as the nadir population size as a proportion of K) (Table 6). Population depletion and recovery was less influenced by the selection of the Ω value. The range of outputs for the three parameters were all centred near the midpoint of the range, indicating that they were being drawn from a uniform distribution (Table 7, Table 8). For the first model, the mean trajectory reaches a nadir level in the mid-1800s and recovers to ca. 6,000 whales in 2011 (a recovery level of ca. 36% for a modelled K of ca. 17,500 (Table 9). Nearly all of the 10,000 iterations either went extinct (66.7%) or recovered (33.0%) (Table 10), suggesting that population trajectories are highly sensitive to small changes in input values.

Establishing parameter ranges for simulation models 2-6

The first model set used values of K and r_{max} that were known to be broader than supported by the available data and initial model results. This was done to explore model behaviour and determine which parameters had the most influence on model trajectories. The remaining model runs considered refined ranges for K while also using a narrower range for r_{max} (0.035-0.045, see Wade 1998; George et al. 2004; IWC 2013). Parameter ranges are summarized in Table 3.

SIMULATION MODELS 2-6

Model diagnostics indicated no significant ($P > 0.05$) correlations between parameter values for each model (Table 4), so all parameters were drawn randomly for each iteration. There was again no significant autocorrelation (at lags of 1 or 2) for values of r_{max}, Ω and K in any model (Table 5), so values for each parameter were randomly drawn for each successive iteration. Population trajectories vary widely and again range from extinction to full recovery across the different model sets. As in model 1, results are summarized in Tables 6 to 10. Mean (plus 95%

CI) and median population trajectories are shown in Figures 4 to 8. Models 2 through 4 continue to refine the parameter range for K (from 16,000-20,000 to 17,000-19,000 to 17,500-18,500) while keeping the r_{max} and Ω ranges constant (0.035 to 0.045 and 1.10 to 1.20, respectively). Model 5 examined a K range at the higher end of the original range (18,000-20,000), and model 6 refines this slightly, to 18,000 to 19,000) (both have the same parameter values for r_{max} and Ω as models 2-4).

PLAUSIBLE ESTIMATES OF K

The mean population trajectories were compared for each of the six models, and compared to available recent population estimates (Figure 9). The various models suggest a carrying capacity (K, pre-commercial exploitation population size) of ca. 18,000-18,500 whales as the most plausible.

MODELS WITH CONSTANT K

To further explore trajectories with K near 18,000, we ran the model three additional times, with the same range for r_{max} and Ω as models 2-6, but with constant K = 18,000, 18,500, and 19,000. Each model was again run for 10,000 iterations (Figures 10, 11). The results again suggest a minimum K of 18,000, and given that recent estimates are considered conservative, K = 18,500 may be a more plausible scenario. We consider K = 18,500 to be a reasonable estimate for setting recovery goals and targets.

DISCUSSION

A series of deterministic Monte Carlo simulations using a standard discrete time logistic growth model suggest that the EC-WG bowhead whale population numbered around 18,500 animals in 1500 AD, just prior to the start of commercial whaling. Commercial exploitation started ca. 1530 with Basque whalers in the Gulf of St. Lawrence and southern Labrador. Estimated Basque harvests peaked in the mid-1500s and then declined soon after (Figure 1, Higdon 2010). The bowhead population quickly declined, but was able to rebound after 1600 when Basque harvests declined. When commercial whaling started off the West Greenland coast in the late 1600s (Higdon 2010), the bowhead population has been able to recover (i.e., ≥ 70% of K, e.g., see Figures 9-11). Population size remained fairly stable, and > 70% of K, throughout the 1700s, despite persistent catches by multiple whaling nations (Higdon 2010, also see Figure 1). In the early 1800s, whaling vessels crossed Baffin Bay and began to hunt bowhead whales in Canadian Arctic waters. Harvests quickly intensified and removals increased by an order of magnitude (Figure 1). This resulted in a precipitous decline in the bowhead whale population, which reached a nadir in the late 1800s. Declines in bowhead availability led to the whaling crews diversifying and going after other species, such as walrus (*Odobenus rosmarus rosmarus*), beluga whales (*Delphinapterus leucas*) and Arctic foxes (*Vulpes lagopus*), to keep voyages profitable (Stewart et al. 2014). This allowed the vessels to continue harvesting small numbers of bowhead whales until the early 1900s, when commercial harvesting ceased (Figure 1). The modelled population(s) show rapid growth during the early to mid-1900s, with a slight reduction in growth rates in recent decades as numbers rise and density-dependent effects start to play a bigger role (Figures 9-11).

COMPARISON WITH PREVIOUS POPULATION MODELLING EFFORTS

There have been previous attempts to model pre-exploitation abundance of bowhead whales, all using less complete catch histories and under a hypothesis of two different stocks. Ross (1974, 1979) compiled bowhead harvests, and these harvest data were used by other authors to back-calculate using a population model to estimate stock size prior to exploitation. Mitchell (1977) devised a simple three-step method to estimate pre-exploitation population sizes of all bowhead whale stocks. The method assumes net recruitment equals zero, so the original population at the beginning of a decade is simply the number killed plus the number remaining. The first step in the calculation involves summing the estimates of the number of whales caught during a decade of peak harvests. The second step is to correct the catch upwards to account for whales struck but lost and presumed to have died. The final step requires estimating the number of whales remaining at the end of the peak decade based on the number of whales harvested in the next few decades. Using the three-step method (Mitchell 1977), the population size of the Davis Strait stock near the onset of commercial exploitation was estimated to be 11,000 (as revised by Mitchell and Reeves 1981 using an updated catch history). The pre-exploitation population size of the Hudson Bay stock was estimated to be ca. 575 (as revised by Woodby and Botkin 1993).

Woodby and Botkin (1993) also used a simple recruitment model (maximum net recruitment rate of 0.05) to estimate pre-exploitation stock sizes of 11,800 for Davis Strait and 450 for Hudson Bay. Catch data were from Ross (1979), and were corrected upwards by 0.15 and 0.20 for Davis Strait and Hudson Bay, respectively, following Mitchell (1977). These estimates all assumed two closed populations in Hudson Bay and Davis Strait/Baffin Bay, which is now known to be incorrect (COSEWIC 2009). These estimates also used catch histories that had lower total removals and did not extend back to include Basque whaling.

More recently, Witting (2011) used the catch history in Higdon (2010) to conduct Bayesian assessments of the EC-WG bowhead whale stock and examined whether population dynamics were best described by density regulated growth or by inertia dynamics. There was substantial statistical support (based on Bayes factors) for inertia dynamics and rejection of density regulated growth. Witting (2011) estimated a population dynamic equilibrium of 30,000 (90% CI: 24,000 - 35,000) whales in 1719. Witting (2011) did not include Basque harvests and pre-1700s Inuit harvests, and the catch series was not corrected for killed but lost whales. If this was done the resulting estimate of K would presumably be higher. Witting (2011) also reported the results of the density regulated growth model, which estimated a population dynamic equilibrium abundance of 16,000 (90% CI: 12,000 - 25,000), which is quite similar to the results of the deterministic modelling we conducted.

COMPARISON WITH RECENT POPULATION SIZE ESTIMATES

Aerial surveys were most recently conducted in 2013, resulting in an estimate of 6,745 whales (CV = 22%) (DFO 2015; Doniol-Valcroze et al. 2015). This survey covered all the major summer aggregation areas of the population except Foxe Basin and Repulse Bay, and it is therefore conservative. Frasier et al. (2015) conducted Bayesian analyses of genetic capture-mark-recapture data (samples collected over the 19-year period 1995-2013) using several analytical approaches, and their best estimate of total population abundance was 7,660 (95% HDI 4,500-11,100). This “best” estimate was based on a 5-year data set, with the rationale being that the population size likely changed throughout the 19 years of sample collection, which could bias estimates. Analyses of the full 19-year dataset resulted in an abundance estimate of 12,220 whales (95% HDI = 8,680-16,200) (Table 2).

Overall, available evidence suggests that the current abundance of bowhead whales numbers in the range of 6,000 to 12,000 animals, and likely towards the mid to high end given that most recent estimates have not included coverage of the entire range. Figure 11 compares model results with recent population estimates. The model does not incorporate these estimates and therefore this can be seen as a test of the models performance. Most population estimates were considered negatively biased due to inadequate survey coverage, with the exception of the genetic capture-mark-recapture study. We conclude that the model performed well with a current population size of between 6-12K whales. A rough estimate of a historic population size of 18.5K and a current population estimate of 10K would indicate that the population is currently at ca. 54% of K.

UNCERTAINTIES IN PARAMETER VALUES

The model could also be run using alternate distributions (e.g., have r_{max} follow a normal distribution with mean 0.04 and standard deviation 0.015), but uniform distributions were used here due to uncertainty with parameter values. In this assessment, we used the best available estimates of r_{max} based on B-C-B whales, which has been well-studied for this stock (George et al. 2004; IWC 2013). These data are assumed to be applicable to the population dynamics of EC-WG bowhead whales, and research on this stock is unlikely to provide refined estimates in the short term. The harvest history we used (Higdon 2010) is reasonably well documented. Gaps in the series are known to occur, and dedicated archival research might help fill in some minor gaps. This work would be unlikely to cause major changes to the harvest series, however, particularly the pattern of expansion and exploitation (i.e., magnitude of harvests and opening of different “fishing grounds”). There are no empirical data on the true value of the shaping parameter (i.e., exponent setting MSYL) in the logistic growth model, but it has been well discussed in the literature (e.g., see Whitehead 2002; Witting 2011). We used $z = 2.39$, which equals MSYL at 60% of K, a conventional assumption for populations of large whales. If MSYL is at a lower percentage of K (e.g., $z = 1.00$ and MSYL = 50% of K), a larger initial population size (K) is needed to sustain harvests. Conversely, if z is higher (e.g., 5.00, equal to MSYL at 70% of K), a smaller initial population size can sustain the known harvests. Killed but lost rates are uncertain, but our range of 10-20% is reasonable for initial parameter estimation based on available data (Mitchell 1977; Mitchell and Reeves 1981; Reeves and Mitchell 1990; Woodby and Bodkin 1993; Reeves and Cosens 2003). The value chosen for the killed but lost correction had the least influence on the model trajectories, but this parameter is also the one that could most easily be updated based on empirical data. As such, the best way to address uncertainty in the short term would be to examine whaling logbooks and try to refine estimates for the killed and lost correction factor.

DIRECTIONS FOR FUTURE RESEARCH

A Bayesian modelling approach could also be used to examine EC-WG bowhead whale population dynamics, and the deterministic model results reported here would help establish a baseline for choosing reasonable priors for parameter values. The deterministic model results can provide guidance in selecting parameter values (and ranges) for a Bayesian population model. However, given the similarities of our results with Witting’s (2011) density-dependent model, a Bayesian formulation may not provide results that are much different. Determining whether inertial dynamics better explain bowhead population growth than density-dependent growth (Witting 2011) may be a fruitful endeavor. However, evidence is accruing to justify density-dependent killer whale predation of bowhead whales as a plausible demographic pattern (Ferguson et al. 2012, Reinhart et al. 2013).

This estimate of K could potentially be refined through archival research on struck and lost rates, which may provide additional information to revise the range of values for this parameter. However, minor modifications in the historical data are unlikely to result in significant changes to model solutions reported here.

The DFO Precautionary Approach uses a single-species target and limit reference points (Stenson et al. 2012). However, for ecosystem-based fisheries management, target species should be considered within the context of the overall state of the ecosystem and include nontarget species (Pikitch et al. 2004). A better understanding of bowhead population dynamics over time could be used in an ecosystem-based model to better understand ecosystem shifts over time (Higdon and Ferguson 2010).

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TABLES AND FIGURES

Table 1. Results from selected fully-deterministic model trajectories with z = 2.39 and different variable combinations for K (10,000 to 25,000), r_{max} (0.030 to 0.050), and Ω (1.10 to 1.20). For all trajectories, the year the population reaches its minimum (nadir) size, nadir population size, and the 2011 population size are shown.

K	r_{max}	Ω	Nadir year	Nadir size	2011 size
10,000	0.050	0.10	1594	Extinct	Extinct
15,000	0.050	0.10	1847	Extinct	Extinct
20,000	0.030	0.10	1882	2,604	19,821
20,000	0.030	0.20	1856	Extinct	Extinct
20,000	0.050	0.10	1834	8,466	19,981
25,000	0.030	0.20	1838	9,103	24,977

Table 2. Recent estimates of the size of the EC-WG bowhead whale stock. The 2002 survey was analyzed multiple times. Results are imprecise due to low number of sightings.

Date of estimate	Estimate	Method	Comments	Source
March 1981	1,349 (95% CI = 402-4,529)	Aerial survey		Koski et al. (2006)
2004	3,633 (95% CI = 1,382-9,550)	Above results projected forward		Koski et al. (2006)
August 2002	7,309 (95% CI = 3,161-16,900)	Aerial survey	Analyzed multiple times	Cosens et al. (2006)
August 2002	14,400 (95% CI = 4,811-43,105)	Aerial survey	See above	Dueck et al. (2008)
August 2002	8,187 (95% CI = 3,835-17,480)	Aerial survey	See above	Heide-Jørgensen et al. (2008)
August 2002	6,344 (95% CI = 3,119-12,906)	Aerial survey	See above	IWC (2009)
August 2002	8,500 (90% CI = 3,900-17,000)	Aerial survey	See above	Witting (2011)
2013	7,660 (95% HDI 4,500-11,100)	Genetic CMR		Frasier et al. (2015)
August 2013	6,745 (CV 22%)	Aerial survey		DFO (2015); Doniol-Valcroze et al. (2015)

Table 3. Summary of input parameter ranges for the six Monte Carlo simulation models.

Model no.	K range	r_{max} range	Ω range
1	15,000 to 20,000	0.030 to 0.050	1.10 to 1.20
2	16,000 to 20,000	0.035 to 0.045	1.10 to 1.20
3	17,000 to 19,000	0.035 to 0.045	1.10 to 1.20
4	17,500 to 18,500	0.035 to 0.045	1.10 to 1.20
5	18,000 to 20,000	0.035 to 0.045	1.10 to 1.20
6	18,000 to 19,000	0.035 to 0.045	1.10 to 1.20

Table 4. Correlation coefficients between parameter values, used as model diagnostics to ensure that parameter values were being drawn randomly for each iteration.

Model no.	K and r_{max}	K and Ω	r_{max} and Ω
Model 1	0.002	0.003	-0.005
Model 2	0.011	-0.087	0.034
Model 3	-0.027	-0.029	0.076
Model 4	0.022	0.046	-0.037
Model 5	0.022	-0.043	-0.001
Model 6	-0.002	-0.004	0.000

Table 5. First- and second-order autocorrelation coefficients for parameters, used as model diagnostics to ensure that values for each parameter were randomly drawn for each successive iteration.

	Lag = 1			Lag = 2		
Model no.	r_{max}	K	Ω	r_{max}	K	Ω
Model 1	-0.006	0.016	0.009	-0.005	0.016	0.009
Model 2	0.017	0.004	-0.029	0.017	0.005	-0.030
Model 3	0.053	0.018	0.053	0.053	-0.003	0.017
Model 4	-0.013	-0.010	-0.024	-0.039	-0.007	0.001
Model 5	-0.049	0.015	-0.017	-0.001	-0.026	-0.041
Model 6	0.007	0.013	-0.002	-0.016	-0.003	-0.018

Table 6. Correlation coefficients for correlations of parameter values and 2011 and nadir population sizes (measured as a proportion of K) for the six models.

	Correlation with 2011 population			Correlation with nadir population		
Model no.	K	r_{max}	Ω	K	r_{max}	Ω
Model 1	0.641	0.433	-0.173	0.643	0.481	-0.190
Model 2	0.777	0.244	-0.279	0.785	0.307	-0.314
Model 3	0.565	0.429	-0.359	0.563	0.464	-0.403
Model 4	0.282	0.646	-0.435	0.279	0.678	-0.477
Model 5	0.465	0.463	-0.397	0.465	0.569	-0.486
Model 6	0.284	0.596	-0.470	0.331	0.670	-0.534

Table 7. Model input ranges for r_{max} and Ω and output from Monte Carlo simulations (10,000 per model) (CL = confidence limit (95% range), Std. Dev. = standard deviation).

		Model output				
	Input range	Mean	Lower CL	Upper CL	Median	Std. Dev.
r_{max}						
Model 1	0.030 to 0.050	0.0400	0.0305	0.0495	0.0399	0.0058
Model 2	0.035 to 0.045	0.0400	0.0352	0.0447	0.0399	0.0029
Model 3	0.035 to 0.045	0.0400	0.0352	0.0447	0.0402	0.0029
Model 4	0.035 to 0.045	0.0400	0.0353	0.0447	0.0401	0.0029
Model 5	0.035 to 0.045	0.0400	0.0352	0.0448	0.0401	0.0029
Model 6	0.035 to 0.045	0.0400	0.0352	0.0448	0.0399	0.0029
Ω						
Model 1	1.10 to 1.20	1.1502	1.1031	1.1974	0.0287	1.1501
Model 2	1.10 to 1.20	1.1499	1.1025	1.1974	0.0288	1.1496
Model 3	1.10 to 1.20	1.1506	1.1026	1.1975	0.0286	1.1491
Model 4	1.10 to 1.20	1.1503	1.1023	1.1977	0.0288	1.1488
Model 5	1.10 to 1.20	1.1501	1.1026	1.1978	0.0287	1.1489
Model 6	1.10 to 1.20	1.1506	1.1027	1.1973	0.0288	1.1507

Table 8. Model input ranges for K and output from Monte Carlo simulations (10,000 per model) (CL = confidence limit (95% range), Std. Dev. = standard deviation).

		Model output				
	Input range	Mean	Lower CL	Upper CL	Std. Dev.	Median
Model 1	15,000 to 20,000	17,495	15,120	19,874	1,445	17,496
Model 2	16,000 to 20,000	18,013	16,091	19,900	1,151	18,009
Model 3	17,000 to 19,000	17,994	17,047	18,950	576	18,069
Model 4	17,500 to 18,500	18,001	17,521	18,472	287	18,009
Model 5	18,000 to 20,000	19,004	18,048	19,951	578	18,918
Model 6	18,000 to 19,000	18,495	18,022	18,972	289	18,493

Table 9. Model input ranges for K and resultant outputs for population nadir and 2011 population size, including recovery level (proportion of K).

		Nadir			2011			
Model no.	Input range	Mean (95% CI)	Std. Dev.	Year	Mean (95% CI)	Std. Dev.	Recovery level	K
Model 1	15,000 to 20,000	2,179 (0-8,810)	2,752	1849	6,205 (0-19,819)	8,828	0.355	17,495
Model 2	16,000 to 20,000	2,619 (0-7,748)	2,473	1849	8,184 (0-19,878)	9,381	0.454	18,013
Model 3	17,000 to 19,000	1,824 (0-9,162)	2,782	1874	6,886 (0-18.912)	8,857	0.383	17,994
Model 4	17,500 to 18,500	1,548 (0-7,976)	2,406	1874	6,459 (0-18,430)	8,629	0.359	18,001
Model 5	18,000 to 20,000	4,370 (1,811-6,818)	1,285	1838	14,724 (0-19,932)[1]	8,007	0.775	19,004
Model 6	18,000 to 19,000	3,026 (0-8,562)	2,637	1865	10,968 (0-18,944)	9,064	0.593	18,495

[1] Lower 95% confidence interval includes extinction starting in 1854

Table 10. Summary of fate of model trajectories for the six models, with input parameter ranges also shown for comparison. Output data is the proportion of model iterations (n = 10,000 that went extinct, the proportion that recovered (≥ 70% of K), the proportion that fully recovered (≥ 90% of K and a subset of the previous category), and the remaining trajectories.

	Input parameter range			Proportion of model iterations			
Model no.	K	R_{max}	SL	Extinct	Recovered	Fully recovered	Rest
Model 1	15,000 to 20,000	0.030 to 0.050	1.10 to 1.20	0.667	0.330	0.328	0.003
Model 2	16,000 to 20,000	0.035 to 0.045	1.10 to 1.20	0.578	0.422	0.419	0.000
Model 3	17,000 to 19,000	0.035 to 0.045	1.10 to 1.20	0.590	0.399	0.394	0.011
Model 4	17,500 to 18,500	0.035 to 0.045	1.10 to 1.20	0.570	0.423	0.419	0.007
Model 5	18,000 to 20,000	0.035 to 0.045	1.10 to 1.20	0.238	0.759	0.754	0.003
Model 6	18,000 to 19,000	0.035 to 0.045	1.10 to 1.20	0.403	0.590	0.585	0.007

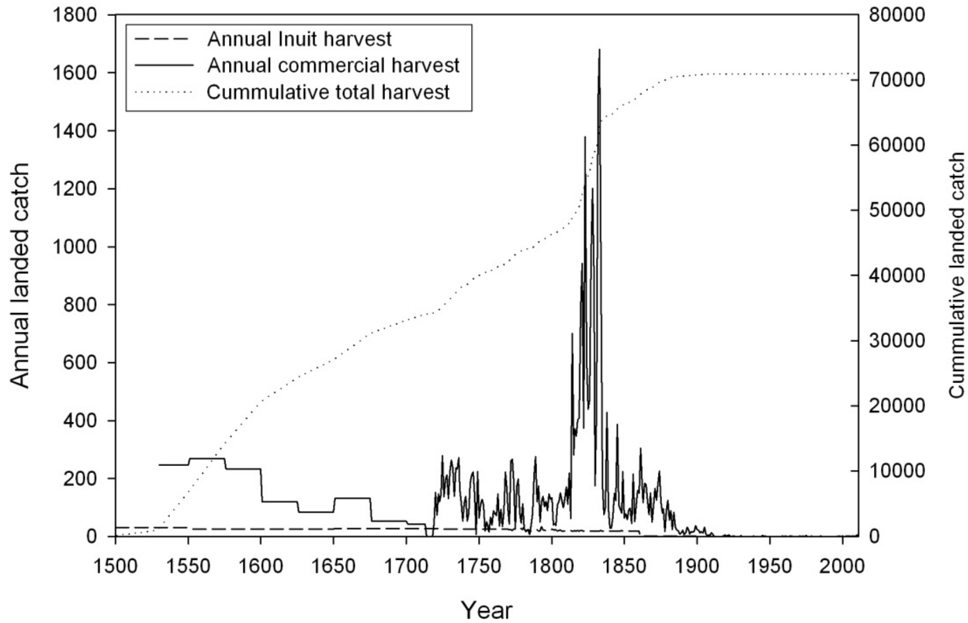

Figure 1. Catch history of EC-WG bowhead whales, from Higdon (2010) and updated as per DFO (unpub.) and Heide-Jørgensen et al. (2012).

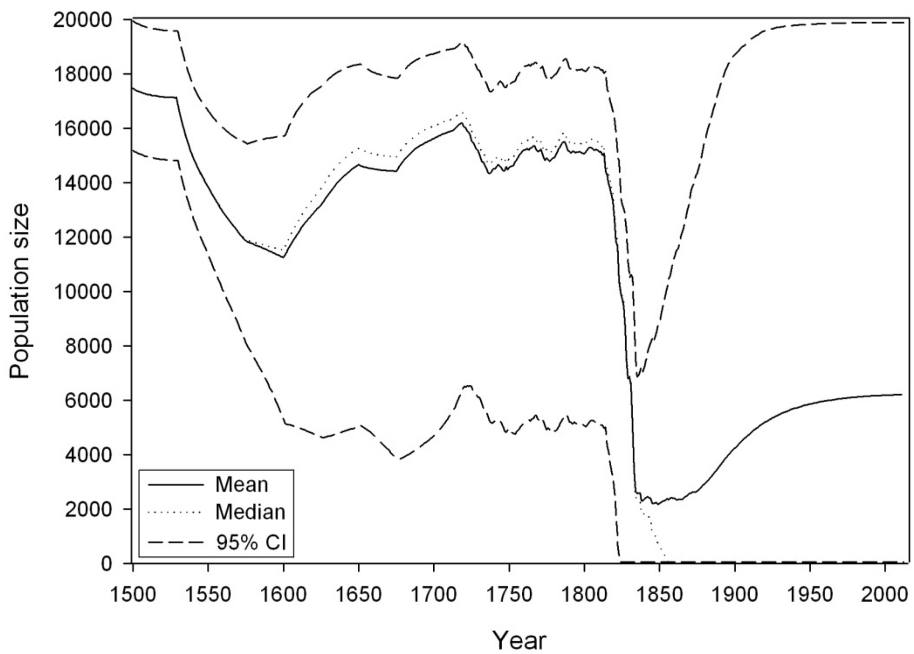

Figure 2. Mean (plus 95% confidence intervals) and median population trajectory from 10,000 iterations of model 1, with input parameter ranges as follows: K = 15,000 to 20,000, r_{max} = 0.030 to 0.050, Ω = 1.10 to 1.20.

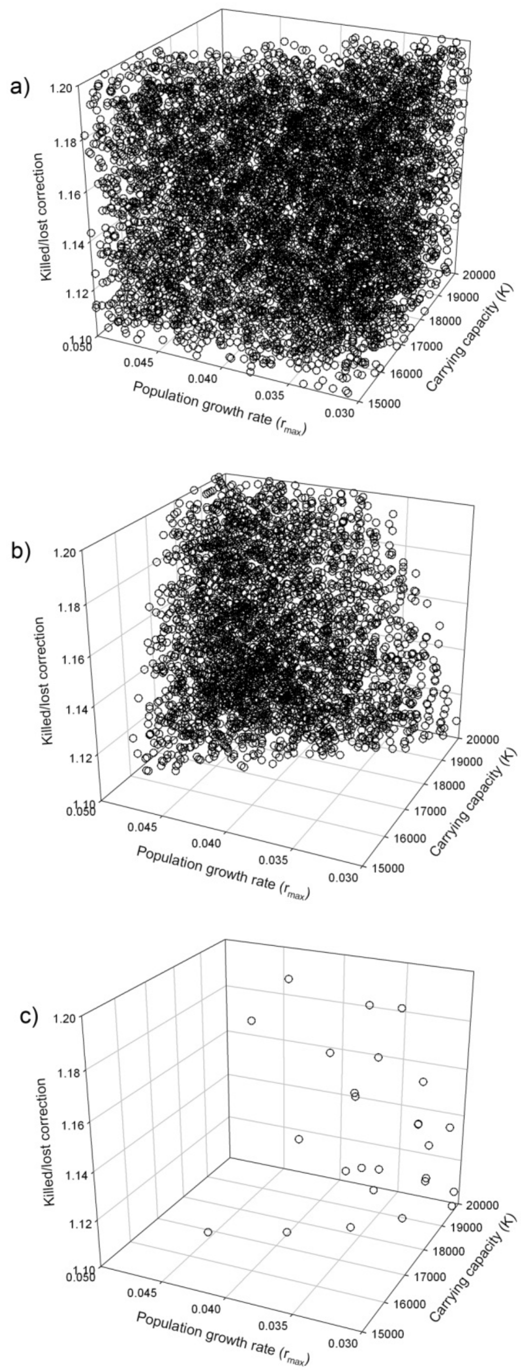

Figure 3. 3D scatter plots of parameter combinations in model 1 that lead to a) extinction (n = 6,674), b) recovery (≥ 70% of K, n = 3,300), and c) neither extinction nor recovery (n = 26).

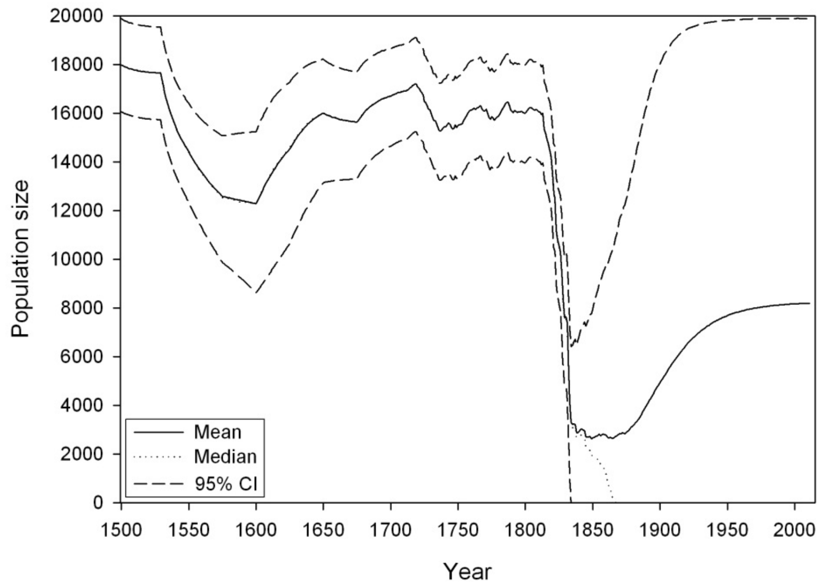

Figure 4. Mean (plus 95% confidence intervals) and median population trajectory from 10,000 iterations of model 2, with input parameter ranges as follows: K = 16,000 to 20,000, r_{max} = 0.035 to 0.045, Ω = 1.10 to 1.20.

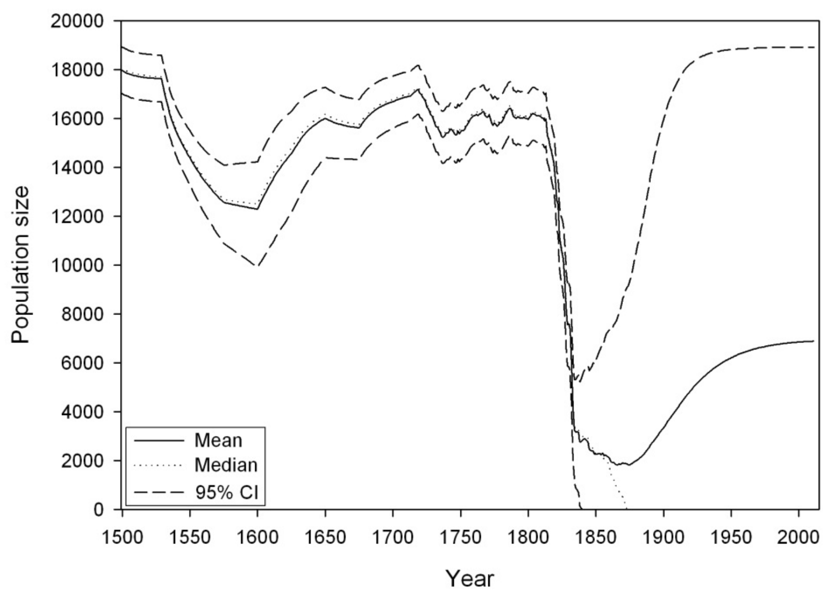

Figure 5. Mean (plus 95% confidence intervals) and median population trajectory from 10,000 iterations of model 3, with input parameter ranges as follows: K = 17,000 to 19,000, r_{max} = 0.035 to 0.045, Ω = 1.10 to 1.20.

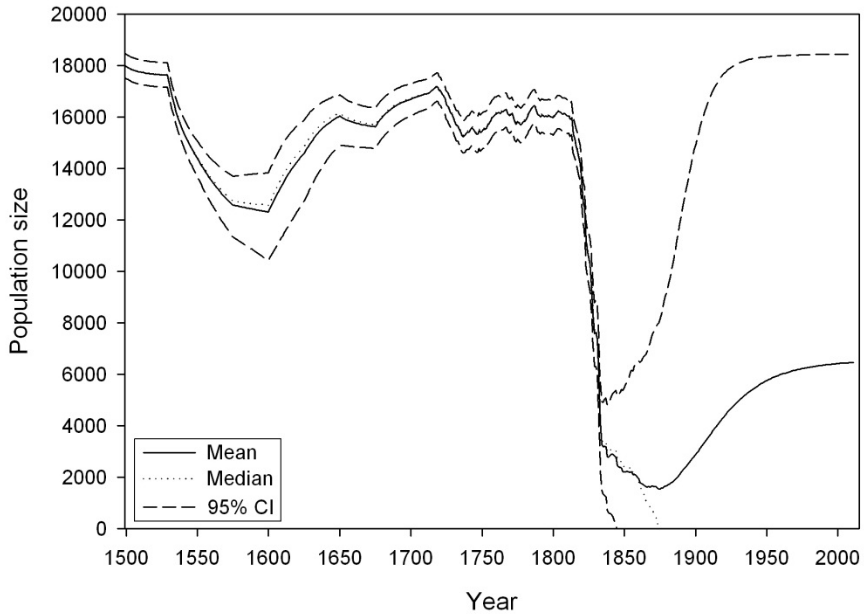

Figure 6. Mean (plus 95% confidence intervals) and median population trajectory from 10,000 iterations of model 4, with input parameter ranges as follows: K = 17,500 to 18,500, r_{max} = 0.035 to 0.045, Ω = 1.10 to 1.20.

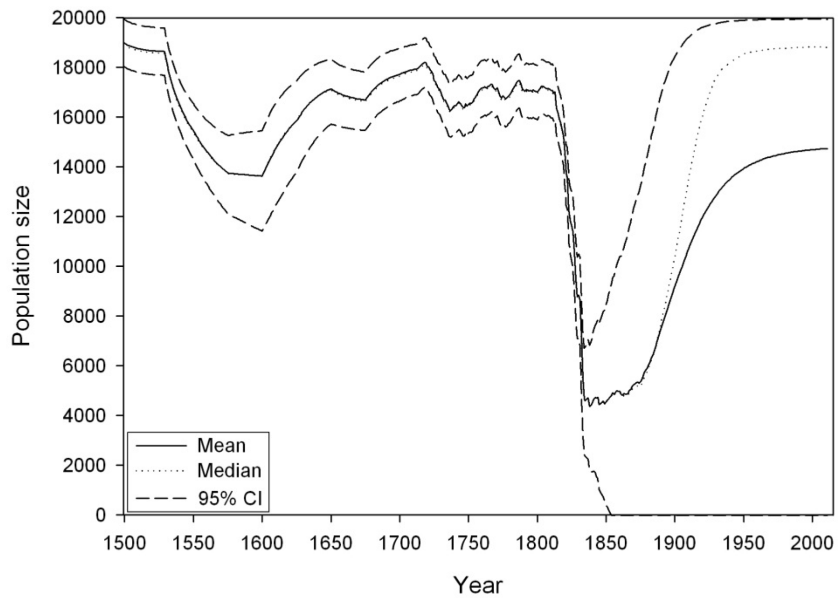

Figure 7. Mean (plus 95% confidence intervals) and median population trajectory from 10,000 iterations of model 5, with input parameter ranges as follows: K = 18,000 to 20,000, r_{max} = 0.035 to 0.045, Ω = 1.10 to 1.20.

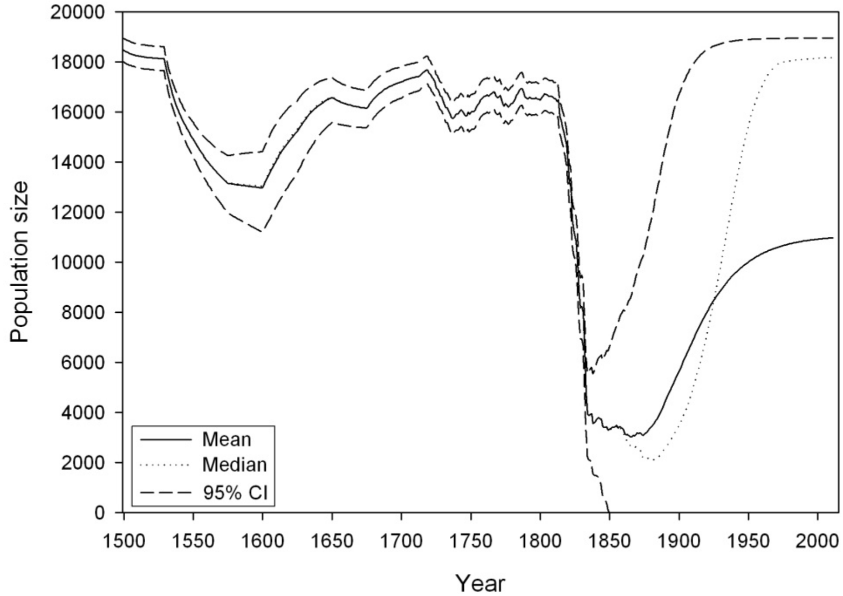

Figure 8. Mean (plus 95% confidence intervals) and median population trajectory from 10,000 iterations of model 6, with input parameter ranges as follows: K = 18,000 to 19,000, r_{max} = 0.035 to 0.045, Ω = 1.10 to 1.20.

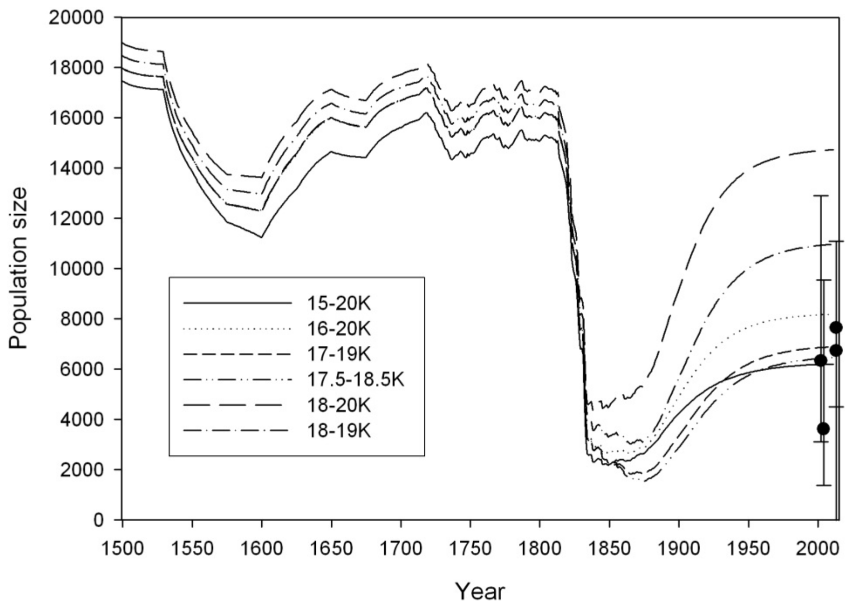

Figure 9. Mean population trajectory for models 1-6, with recent population estimates for comparison. Model 1 had r_{max} = 0.030 to 0.050 and Ω = 1.10 to 1.20, all other models had r_{max} = 0.035 to 0.045 and Ω = 1.10 to 1.20.

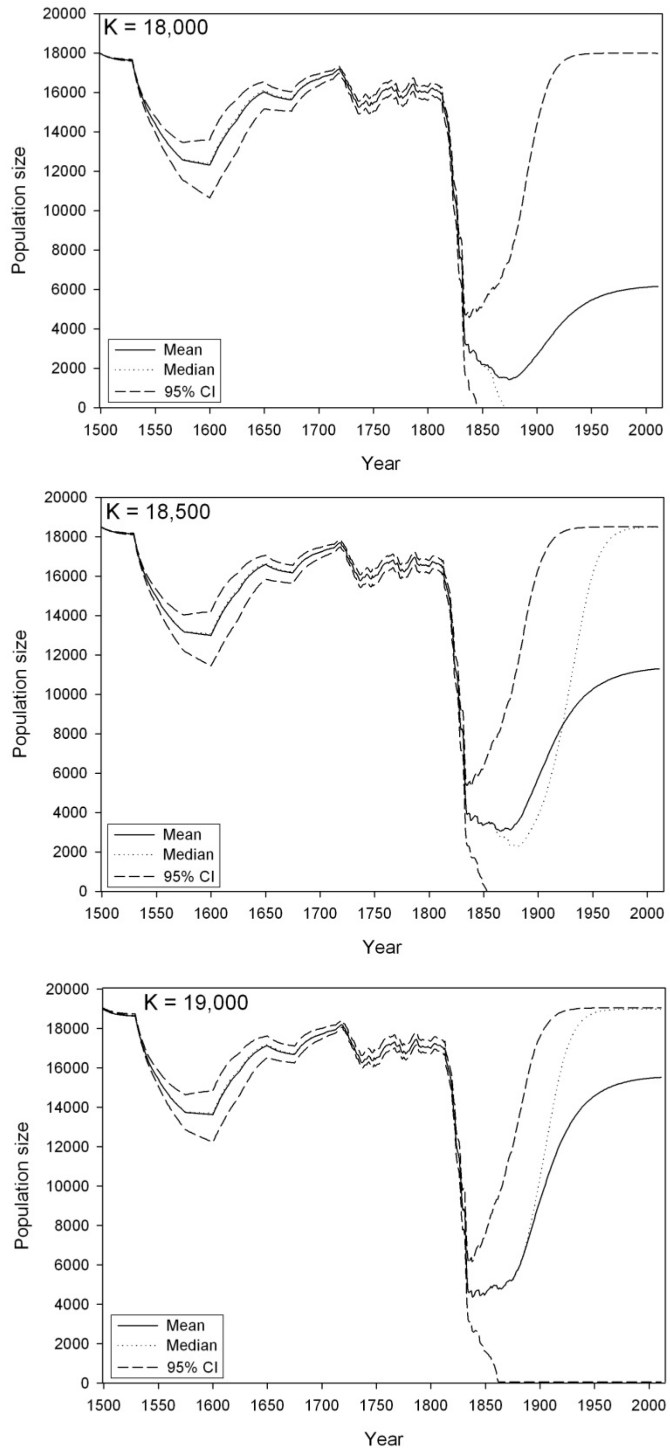

Figure 10. Mean (plus 95% confidence intervals) and median population trajectory from 10,000 iterations of models with constant K = 18,000, 18,500, and 19,000, using same range for r_{max} and Ω as models 2-6.

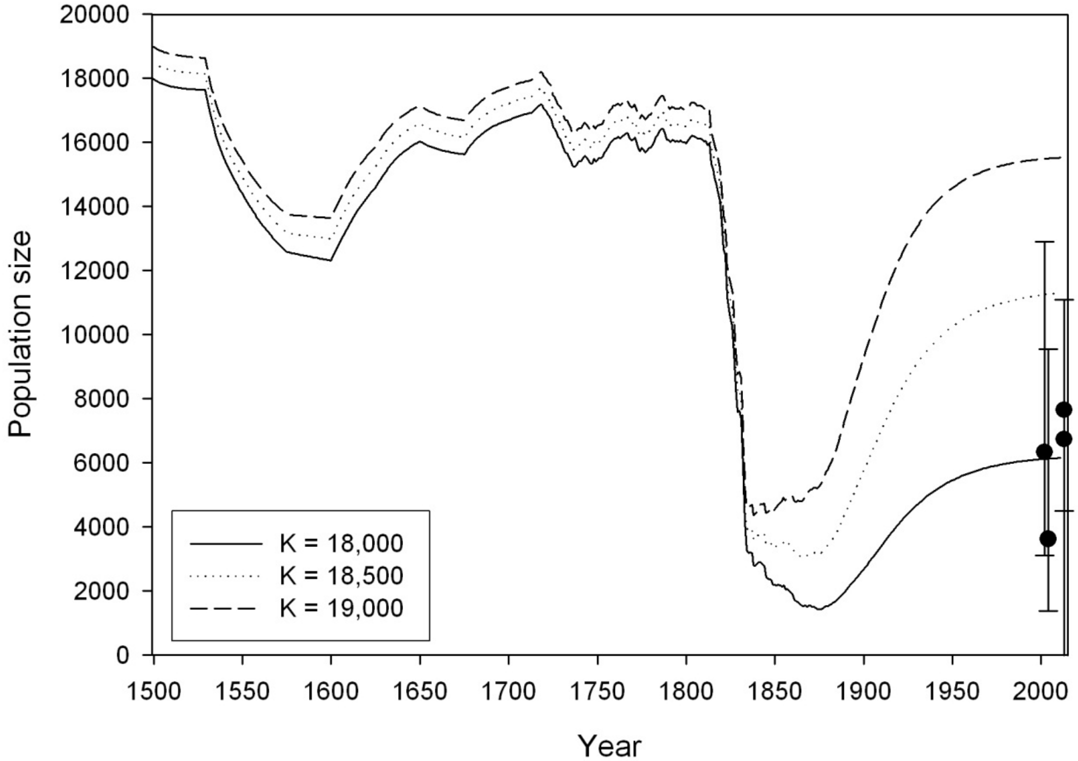

Figure 11. Mean population trajectory for three models with constant K, with recent population estimates for comparison.