Fisheries and Oceans Canada
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Sciences des écosystèmes
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Canadian Science Advisory Secretariat (CSAS)

Research Document 2017/027

Quebec Region

Predicting responses of St. Lawrence beluga to environmental change and anthropogenic threats to orient effective management actions

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April 2017

Foreword

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

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

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

ISSN 1919-5044

Correct citation for this publication:

Williams, R., Lacy, R.C., Ashe, E., Hall, A., Lehoux, C., Lesage, V., McQuinn, I., Plourde, S. 2017. Predicting responses of St. Lawrence beluga to environmental change and anthropogenic threats to orient effective management actions. DFO Can. Sci. Advis. Sec. Res. Doc. 2017/027. v + 44 p.

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ABSTRACT

The St. Lawrence Estuary ("SLE") population of beluga (*Delphinapterus leucas*) was depleted by hunting. The population failed to increase in numbers at the rate one would expect after cessation of hunting. We conducted a population viability analysis ("PVA") to quantify factors that most likely limit recovery of SLE beluga. The main threats considered were: changes in prey abundance; changes in foraging efficiency caused by underwater noise and disturbance; and chemical pollution, namely polychlorinated biphenyls ("PCBs"). Although all three threats have received scientific and management attention, there is greater evidence available to quantify the relationships between prey and demography than between noise or PCBs, and demography. The primary objective was to use best available science to build a framework to predict how the population might respond to changes in environmental conditions and varying levels of the three main anthropogenic threats. This tool will provide information on the relative importance of each threat (across a range of input values), and identify knowledge gaps needed to be filled in order to improve mitigation and monitoring of effects, and research activities. As the quantity and quality of data on the three threats and demography increase, the tool will allow end-users to explore the likely fate of the population under alternative management actions to mitigate threats. Having built a framework that simulates how big a given population-level effect might be at varying levels of anthropogenic threats, a discussion among scientists and managers is needed next to gauge where we think the population might be along the spectrum for each threat. This may include identifying plausible ranges for threats that might have existed in the past and may have influenced demographic parameters. This will inform threat scenarios that might exist in the future, either under climate change predictions or due to management actions.

Across the range of stressors we considered, data were only available to link threats to changes in calf mortality. Additional research is needed to assess whether stressors could influence pregnancy or adult mortality. Uncertainty in current demographic rates, especially adult mortality, and their functional relationships to environmental conditions and threats together contributed twice as much to our uncertainty in the future trajectory of the population as did the ranges of possible management actions that were considered. The effects of prey availability contributed most to changes in calf mortality, followed by noise and PCBs. The report outlines important caveats with all three threats, which may influence the relative importance of each. Although we considered management scenarios that reduced threats singly and in combination, no management scenario resulted in the population reaching a previously identified recovery target of 7,070 individuals by 2100.

Prédiction des réponses du béluga du Saint-Laurent aux changements environnementaux et aux menaces anthropiques afin d’orienter des actions de gestion efficaces

RÉSUMÉ

La population de bélugas (*Delphinapterus leucas*) de l’estuaire du Saint-Laurent (ESL) a été décimée par la chasse. La population a failli à s’accroitre en nombre au taux attendu après l’arrêt de la chasse. Nous avons mené une analyse de viabilité de la population (“PVA”) pour quantifier les facteurs limitant le plus probablement le rétablissement des bélugas de l’ESL. Les menaces principales qui ont été considérées étaient: les changements de l’abondance des proies; les changements dans l’efficacité à s’alimenter en raison du bruit sous-marin et du dérangement; la pollution chimique, notamment les biphényles polychlorés (“BPCs”). Bien que les trois menaces aient reçu un certain niveau d’attention par les scientifiques et la gestion, il existe de plus grandes évidences afin de quantifier les relations entre les proies et la démographie qu’entre le bruit ou les BPCs et la démographie. L’objectif premier était d’utiliser les meilleures connaissances scientifiques disponibles pour construire un cadre afin de prédire comment la population pourrait répondre à des changements des conditions environnementales et différents niveaux des trois menaces principales. L’outil fournira de l’information quant à l’importance relative de chaque menace (pour un éventail de valeurs possibles), et identifiera les lacunes de connaissance devant être comblées afin d’atténuer, monitorer ou documenter scientifiquement leurs effets. À mesure que la qualité et la quantité de données relatives aux trois menaces et à la démographie augmentent, l’outil permettra les utilisateurs d’explorer le sort de la population en fonction d’actions de gestion alternatives pour atténuer les menaces. Une fois qu’est en place le cadre permettant de simuler l’ampleur que peut prendre un effet au niveau de la population selon divers niveaux de menace anthropiques, il est ensuite nécessaire d’engager une discussion entre les scientifiques et les gestionnaires afin d’évaluer où se situe la population le long du spectre de chaque menace. Ceci peut inclure d’identifier l’étendue plausible des menaces qui ont pu exister par le passé et qui ont pu influencer les paramètres démographiques. Ceci alimentera les scénarios concernant les niveaux de menaces qui pourraient exister dans le futur dans le contexte des prédictions du changement du climat ou en raison d’actions de gestion.

Pour l’ensemble des stresseurs que nous avons considérés, seuls des données spécifiques à la relation entre les changements des menaces et ceux de mortalités des veaux étaient disponibles. De la recherche additionnelle est nécessaire afin d’évaluer si les stresseurs peuvent influencer la gestation et la mortalité des adultes. L’incertitude associée aux paramètres démographiques actuels, particulièrement la mortalité chez les adultes, et à leur relation fonctionnelle avec les conditions environnementales et les menaces ont ensemble contribué deux fois plus à l’incertitude sur la trajectoire future de la population que l’incertitude introduite par l’étendue des valeurs considérées en termes d’actions de gestion. Les effets ayant contribué le plus aux changements dans la mortalité des veaux, étaient d’abord la disponibilité des proies, suivi du bruit et des BPCs. Le rapport présente d’importantes mises en garde pour les trois menaces, qui peuvent influencer l’importance relative de chacune. Bien que nous avons considéré des scénarios de gestion qui réduisaient les menaces en les considérant individuellement ou ensemble, aucun scénario de gestion n’a permis à la population d’atteindre l’objectif de rétablissement de 7 070 individus en 2100 établi précédemment.

INTRODUCTION

The St. Lawrence Estuary ("SLE") population of beluga (*Delphinapterus leucas*) has been depleted, in large part, by the legacy of harvests which ended in the late 1970s (Pippard 1985). Many populations of whales have recovered from whaling, but the SLE beluga population did not show the increase in numbers that one might expect after cessation of hunting (Hammill 2007). The population was thought to be relatively stable since 1988 when regular monitoring was initiated, and to number approximately 1,100 individuals in 2005 (DFO 2012). However, unusually high mortality of newborn calves in 2008, 2010 and 2012 triggered a new review of the status of the population and potential treats to its recovery (DFO 2014b). Incorporation of multiple sources of data in a population model indicated that the SLE beluga population was stable or slowly increasing until the early 2000s, and has been declining since then at a rate of approximately 1% per year (Mosnier et al. 2015). Based on this information, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), which has been monitoring the status of SLE beluga for decades, has recommended a status of Endangered instead of Threatened for this population (COSEWIC 2014). The St. Lawrence Estuary ("SLE") population of beluga (*Delphinapterus leucas*), which was listed as Threatened under Canada's Species At Risk Act since 2005 ("SARA", DFO 2012), is now being reclassified Endangered under SARA (Canada Gazette, Part 1, August 27, 2016).

The SLE beluga population is exposed to multiple stressors as it lives downstream of heavily industrialized regions and in a major waterway where shipping and whale-watching activities are intense (DFO 2012; McQuinn et al. 2011). Managers and scientists at Fisheries and Oceans Canada (DFO) are interested in identifying factors that most likely limit the recovery of SLE beluga so that DFO can improve their mitigation, monitoring and research programs. Scientists familiar with beluga have identified a number of processes that may have caused population decline and threaten recovery, including some that are outside of management control (e.g., climate change (including effects of climate change on prey species), ice conditions, sea surface temperature, harmful algal blooms), as well as local anthropogenic threats that may lend themselves to mitigation (e.g., catch quotas for prey species, noise and disturbance from vessels, and contamination from polychlorinated biphenyls (PCBs) and other contaminants) (DFO 2012; DFO 2014a; Plourde et al. 2015). In any endangered species recovery and action plans, it is useful to evaluate where management actions would do the most good for wildlife at the lowest societal cost. When a population faces multiple stressors, it is important to compile quantitative information on population responses to changing environmental conditions in order to guide evidence-based decisions (Williams et al. 2016).

Although the threats are well documented, scientific advice is needed on the relative importance of each threat, because mitigating each threat would involve different audiences, costs and timelines. Unfortunately, the demographic consequences of varying prey abundance have been studied better than the demographic consequences of PCBs or underwater noise and disturbance. As a result, quantitative relationships have been derived to describe the relationships between prey abundance and demography, but the effects of noise and contaminants remain hypotheses to test as new data become available. One way to proceed in such a case is to construct models based on expert opinion. However, an explicit treatment of the uncertainty associated with that approach would result in predictions with such broad confidence intervals that they would be of no practical use in management. Instead, we conducted a population viability analysis (PVA) of the fate of the SLE beluga population across fairly realistic ranges of the threats. After quantifying population-level effects as functions of anthropogenic threats, a discussion among scientists and managers is needed next to gauge the most likely level of each threat – now, as well as in the past or under future management scenarios. The result is therefore a quantitative framework with tentative results to orient future research and management activities, rather than a fully parameterized model with definitive results.

A PVA offers a powerful way to combine data on the demography of a population, with associated measures of uncertainty, along with hypotheses relating to threats that are not well quantified. A PVA encompasses a class of analytical methods that uses demographic modelling to assess risks to wildlife populations, and explore the likely outcomes of (often competing) conservation actions (Burgman et al. 1988; Burgman et al. 1993; Colyvan et al. 1999; Lacy 1993; Lacy et al. 2014). A PVA is well suited to exploring how a population such as SLE beluga might respond to changing environmental conditions, or to alternative management actions. In this study, we constructed a PVA to organize the information available on well-studied demographic rates and hypotheses describing population responses to anthropogenic threats.

MATERIALS AND METHODS

VORTEX POPULATION MODELS

Overview

A population viability analysis (PVA) usually starts with standard demographic analysis ("life table analysis") to make deterministic projections of the expected population growth rate from the mean birth and death rates (Caswell 2001). PVA then extends standard demographic projections in two important ways:

1) the impacts of forces external to the population (e.g., changing habitat conditions; impacts of disease or contaminants; incidental killing) on the demographic rates are explicitly considered and evaluated, and
2) uncertainty in the population trajectory caused by intrinsic (e.g., demographic stochasticity, limitations in local mate availability or other density dependent feedbacks, inbreeding impacts) and extrinsic (e.g., environmental variation, occasional catastrophes) stochastic factors can be explicitly modelled through simulation modelling.

The outputs of PVA include any desired measure of population performance, but commonly assessed metrics include projected mean population size (N) over time, population growth rates (r), expected annual fluctuations in both N and r, probability of population extinction, and quasi-extinction (the likelihood of N falling below any specified number). These outputs can be used to assess risk (e.g., for listing under the Species at Risk Act or other protective regulations), assess vulnerability to possible threats, and determine the suites of actions that would be needed to achieve stated resource protection or restoration goals. They also offer a powerful way to explore the likely timeframe for reaching a recovery target under various scenarios. PVA can be used to explore the likely outcomes of mitigating anthropogenic threats, either singly or in combination, under various action planning scenarios. Because of this, PVA has become a key tool in conservation science and resource management (Morris and Doak 2002).

PVA population models can be constructed in Vortex (Version 10; Lacy et al. 2014; Lacy and Pollak 2013) as an individual-based simulation model. Individual-based simulations let the population-level effects emerge from more detailed descriptions of individual processes. Vortex models population dynamics by stepping through this series of demographic events that describe an annual cycle: mate selection, reproduction, mortality, dispersal, incrementing of age by one year, any incidental removals from the population, and any anthropogenic influences on the previously mentioned demographic processes. Population-level outcomes are then projected as the aggregate fates of all individuals in the population. The simulations are iterated to generate the distribution of fates that the population might experience.

To obtain estimates of the predictability of the fate of a population under a specified description of the population vital rates and environmental conditions, simulation models are repeated many times to generate a distribution of results. This thereby allows calculation of the probability that an outcome will fall outside of an acceptable range. Population-based simulations are most useful when individual characteristics and impacts can be averaged across the population without loss of ability to model key processes of interest. This occurs when populations are large enough so that chance variation among individuals is not a significant contributor to uncertainty. Individual-based models are most useful for assessment of populations with a relatively small number of individuals in a specific and well-described environmental and management setting.

Detailed demographic data are a requirement for any PVA model to provide sufficiently accurate and robust projections to allow estimation of population performance. Model input is required from the focal population or comparable reference populations for mortality rates, aspects of reproduction (e.g., age of breeding, inter-birth intervals, calf survival, or composite measures such as overall fecundity), population size, and habitat carrying capacity – as well as the natural fluctuations in these rates. The difficulty in obtaining sufficient demographic data on endangered or protected species is a common challenge to the usefulness of PVA models, and many practitioners consequently recommend that PVA models be used only to provide assessments of relative risk and relative value of management options, rather than absolute measures of population trajectories.

Sensitivity testing

The PVA models are used to determine which parameters have the greatest leverage on population trajectories. Because demographic rates and environmental conditions can never be known with absolute precision, it is important to test if alternative values of uncertain PVA parameters would lead to substantially different overall conclusions about population status or trend. In addition, PVA models can help identify which threats to prioritize for management to maximize the likelihood of success, and which population parameters should be monitored to maximize the chances of detecting whether mitigation measures or management actions achieve the desired population-level effect.

Uncertainty can be examined in two ways in a PVA model. First, one can enter estimates of various parameters across a range of plausible values, and repeat analyses to test what the estimate would be if the true value were other than the initial estimate. In this approach, alternative estimates of key parameters are tested in simulations of different scenarios. This approach is most useful when the focus is on just few alternative estimates of a few key parameters. Alternatively, values for key uncertain parameters can be randomly sampled by the model itself from their likely ranges within a single scenario of the model. By allowing the values to vary among repeated simulations of the system, the distribution of outcomes from this scenario will encompass both the inherent unpredictability of the natural system and our uncertainty about the key properties of that system. This approach is most useful when there are a number of uncertain parameters to be explored, and when the uncertainty in each is described by a distribution rather than by a few discrete alternatives. It is often useful to use both approaches – sampling parameter values from distributions for a number of uncertain inputs, but then running also several scenarios that contrast alternative possible assumptions, states, or management strategies.

Using PVA model to quantify threats

PVA models were developed initially for quantifying future risk to populations that are vulnerable to collapse due to a combination of threatening processes (Shaffer 1990). As the methods evolved, it was found that PVA predictions are generally more reliable for assessing relative risk of decline or extinction than absolute probabilities (Beissinger and McCullough 2002). This makes PVA models especially useful in identifying conservation actions most likely to achieve conservation goals. One can estimate the population-level effect of an externally imposed stress by comparing demographic measures in the presence or absence of the stress, and to determine what actions would be needed to reverse the impact. The PVA forecasts can then be used to set management targets for expected performance under proposed action plans. Because a PVA can include both inherent uncertainty in the system (e.g., natural variation in the environment) and our uncertainty in the parameter values used in the projections (e.g., uncertainties of demographic rates, baseline conditions, and impacts of the stresses), outputs can be stated with an associated level of confidence, and the uncertainty in the outputs can be partitioned into that component due to natural variation and those components due to our uncertainty about each parameter value.

PVA model for SLE beluga

A Vortex model was constructed to simulate the effects of both intrinsic demographic rates and environmental and anthropogenic stressors on the SLE beluga population. We used a modified version (10.2.1) of Vortex that supports the use of R scripts to calculate model parameter values from predictor variables.

An initial PVA was constructed with the following as inputs:

- One population simulated for 100 years for 10,000 iterations
- Extinction defined as no males or no females
- No adjustment for inbreeding depression, because initial population size was large enough to make significant inbreeding unlikely for a long-lived species
- Maximum lifespan was set to 75, with reproductive senescence of females set to a mean of 50
- Mating system assumed to be polygynous, with new selection of mates each year
- Females assumed to be sexually mature (capable of producing their first calf) as early as age 8, with individual females modelled as being sexually mature beginning at age 8 to 12 (therefore usually producing their first calf by 14 years, based on the breeding rate of mature females, below, of 32.6% per year)
- Females are assumed to cease breeding at between age 45 and 55
- Males assumed to breed from age 12 to the maximum age, with individual males capable of starting breeding at age 12 to 22
- Mortality rates were obtained from Mosnier et al. (2015), with uncertainties in the rates estimated as ¼ of the 95% confidence interval for each parameter estimate.
- Maximum levels of annual variability ("environmental variation": EV) in breeding and mortality rates were obtained by removing expected sampling error from the SD across the more variable years 1999-2012 (Mosnier et al. 2015). See Lacy et al. (2014) for the methods to remove sampling error from estimates of EV.
- Maximum age of survival: 75
- Sex ratio (percent males) at birth: 50
- Carrying capacity set to 8,000 (i.e., somewhere between the DFO recovery target of 7,070 and the 8-10,000 estimated to have been in the population in the 1800s). Note

that the PVA was insensitive to this somewhat arbitrary choice, because the trajectory never reached 8,000.

The rationale for the choice of these and all other demographic parameters is given in Table 1, unless otherwise specified.

Table 1. Parameters used as inputs to program Vortex for the initial population model.

Parameter	**Value**	**Source**	**Notes**
Female age at first reproduction	range: 8-14	Brodie 1971; Sergeant 1973; Heide-Jørgensen and Teilmann 1994	
Male age at first reproduction	range: 12-22	Brodie 1971; Sergeant 1973; Heide-Jørgensen and Teilmann 1994; Finley et al. 1982	
Female age of senescence	range: 45-75	Burns and Seaman 1985	Alaska
Sex ratio at birth	50:50		
Maximum age of survival	75	Lesage et al. 2014	
Males in breeding pool			Assumed to be polygynous
Maximum number of litters per year	1	Lesage and Kingsley 1998	
Maximum number of progeny per litter	1	Lesage and Kingsley 1998	
% adult females that breed each year	0.326 (CI 95% = 0.276-0.369)	Mosnier et al. 2015 See also: Kleinenberg et al. 1964; Sergeant and Brodie 1975; Burns and Seaman 1985; Doidge 1990	Source: Table A.1
Environmental Variation (EV) in breeding	range: 0-0.12	Mosnier et al. 2015	Upper end is the SD in the predicted % of pregnant females during the most volatile period in the time series (i.e., 1999-2012)

Parameter	Value	Source	Notes
Adult mortality rate	median: 0.061 (CI95%: 0.050 – 0.072)	Mosnier et al. 2015 see also: 6.5%=Lesage and Kingsley 1998 7%=Burns and Seaman 1985 8.4%= Doidge 1990 3−8%=Luque and Ferguson 2010	Value based on Mosnier et al. 2015, Table A.1, M3
Calf mortality rate	median : 23.7% (CI95%: 0.165-0.327)	Mosnier et al. 2014	Median from Beta distribution
Environmental Variation (EV) in calf mortality	range: 0-0.12	Mosnier et al. 2014	Upper end is the SD in calf mortality during the most volatile period in the time series
Initial population size	900	Mosnier et al. 2014	Estimate for 2012, rounded to the nearest 100 individual
Carrying capacity	8000	DFO Recovery Strategy (DFO 2012)	Assumed to be larger than the recovery target (7070), but smaller than the largest observed population size (8-10,000)

The three threats considered are the anthropogenic threats identified in the recovery plan (DFO 2012), and the latest status review (DFO 2014b), namely: prey limitation (“prey”); PCBs and other contaminants (“contaminants”); and reduced prey acquisition via disturbance and acoustic masking from underwater noise of boats and ships (“noise”). The analytical approach to integrating natural demographic processes and anthropogenic threats, including uncertainty, is described below.

In addition, changing climatic conditions may be contributing to decline or hindering recovery of the beluga population (DFO 2014b). Water temperatures (SST) have been increasing, while duration of ice cover has been decreasing (Galbraith et al. 2015). Mechanistic models linking changes in SST and ice cover to changes in marine mammal strandings have been explored previously (Truchon et al. 2013). Although these environmental factors are not amenable to control by local management authorities, we can include these effects in our PVA models so as to project how they could be impacting the SLE beluga population.

Generalized additive model of effects of environmental factors and prey

A Generalized Additive Model (GAM) was used to describe inter-annual variability in calf mortality as nonlinear functions of sea-surface temperature in beluga summer habitat (SST), duration of ice cover (ICE) in the Gulf of St. Lawrence (GSL), and abundance of prey (spring herring [HER] and 4T demersal fish [DEM] biomass) (Appendix 1). As SST in the SLE beluga summer habitat is not correlated to ice cover duration in the GSL during the winter, both variables were considered as independent indices of winter and summer environmental conditions in the beluga habitat. The GAMs were fitted using all combination of four variables or less having a known or assumed effect on beluga demographic parameters. Candidate models were compared using the AIC corrected for small sample size. The final selected model corresponded to the lowest AIC (Appendix 1). Using the beluga population data presented in previous analyses (Mosnier et al. 2014), the GAM analyses found that calf mortality over the time period from 1990-2012 was significantly affected by the combination of these environmental parameters (see Figure 1 and text below for a complete description of effects used in PVA). Other demographic rates (fecundity and adult mortality) were not shown to be affected (Appendix 1). (Data from the years 1993 and 2003 were excluded when fitting the GAM because DFO felt that the estimates of large demersal prey biomass for those two years were likely to be highly inaccurate due to abnormal bottom trawl catchability.) To express the predictor variables on a consistent scale that is more intuitive when exploring scenarios and management options, for graphical displays we re-scaled each variable to a 0 to 1 scale, with 1 being the maximum biomass reported in the 1990-2012 data set.

The GAM predicted a U-shaped relationship between ice duration and calf mortality (Figure 1), suggesting that calf mortality would be high when there is either too much or too little ice, and there is an optimum ice condition at which calf mortality is expected to be the lowest (Figure 1). There are no known causal biological mechanisms that could explain this U-shaped relationship, meaning that causes for this relationship could only be hypothesized. However, it has been shown that beluga females tend to avoid very low or very high ice cover in the fall in the Canadian Arctic Archipelago, suggesting that extreme ice cover might not be optimal for the species (Barber et al. 2001). Based on this later study and our GAM results, we hypothesized that average ice conditions in the Estuary and Gulf of St Lawrence would represent optimal winter habitat conditions for SLE beluga. Additionally, the potential for prey to concentrate in the marginal ice zone in the region (Fréchet 1990), and influence of sea ice on biomass and timing of spawning of some beluga prey (e.g., Buren et al. 2014) suggests that the occurrence of sufficient ice edge habitat during years of average ice conditions (and minimal during years of very low and very high ice coverage) could also positively affect pregnant beluga females in winter and lessen calf mortality during the following summer (Truchon et al. 2013). Elevated SST in the summer months is also predicted to have a strong positive effect on calf mortality (Figure 1).

Initially, the GAM also generated a U-shaped relationship of mortality to demersal prey, with predicted mortality increasing at low and high levels of prey (not shown). The increase at high levels of prey was treated as a spurious effect, as the confidence interval around the predicted mortality becomes very large at higher levels of demersal fish biomasses. To prevent this biologically counter-intuitive effect and instead enforce a threshold model of prey biomass on mortality, we specified in the model that demersal biomass is constrained to not exceed the value that leads to the lowest predicted value for mortality (Figure 1) (Plourde et al. 2014). Finally, GAM predicted an inverse relationship between spring herring biomass (HER) and calf mortality (Figure 1).

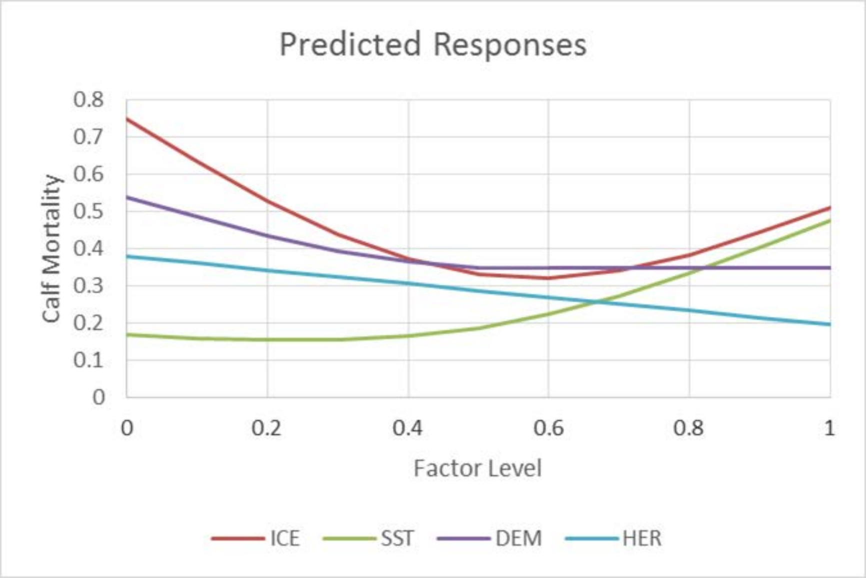

Figure 1. GAM predictions for levels of each predictor variable varied across the range of observed values. The "Factor Levels" on the x-axis are scaled such that they range from the lowest value reported from 1990-2012 in the data set (Level = 0) to the highest value reported (Level = 1). Responses to each predictor variable are shown when the other three variables are held at their "Management Baseline" scenario level (see text below).

We modified the Vortex software code to allow the population simulation to call the "predict.gam" function in the R library "mgcv" (Wood 2016) to predict estimates of calf mortality from the fitted GAM with predictors SST, ice duration, and herring and large demersal fish biomasses. We also used the R script to provide the standard errors (SE) in these predicted values. Thus, the calf mortality rate applied in each year of the simulation had two sources of variation reflecting our uncertainty in the rate. First, at each year of the simulation, the values for environmental and prey variables were sampled from normal distributions that describe the variation observed over time. Second, these sampled values for environmental and prey variables were then entered into the GAM to calculate a mean and standard error for the predicted mortality rate. The mortality rate used that year in the model was then sampled from this predicted mean and SE. This means that the variation in mortality rate in the simulation model encompassed both the temporal variation in the estimates of environmental and prey abundance variables and our uncertainty in the relationship of mortality to those variables.

To explore the influence of each of the four GAM predictor variables on the population trajectory, we ran scenarios that varied each predictor from its lowest value to its highest value observed since 1990. The environmental variables reflecting climate change are not amenable to management at the local level, but the tests of influence of spring herring and 4T demersal fish biomass serve also to test the extent to which population recovery might be achieved by improving the prey biomass.

Prey

Using the data presented in previous analyses (Mosnier et al. 2014), and the GAM (Appendix 1), we included the effects of spring herring and demersal prey biomass on calf mortality (while including also the effects of SST and duration of ice cover; see above). With these relationships, it is possible to model the fate of SLE beluga if prey were to increase or decrease relative to historical average levels. As a starting point for investigating the benefits to increasing prey, therefore, we tested scenarios for each type of prey in which we varied the biomass up to the maximum that has been observed (i.e., prey index = 1).

Noise

Modelling population consequences of noise on marine mammals requires some mechanistic link between behavioral responses or acoustic masking and reductions in some vital rate, mediated by energetic or hormonal pathways (National Research Council 2005). There is a growing body of literature linking vessel traffic to reduced foraging behavior in humpback (Blair et al. 2016) and killer whales (Lusseau et al. 2009; Williams et al. 2006). Anthropogenic noise reduce the acoustic space of SLE beluga (Gervaise et al. 2012), and the latter change their vocal behaviour in response to vessel traffic (Lesage et al. 1999). However, it is not yet possible to link a received level of noise to a known proportional reduction in foraging behaviour or prey intake in the form of a dose-response curve. In order to predict population consequences of underwater noise, we considered some currently unspecified process by which noise reduces the prey available to belugas either spatially or temporally through acoustic masking of biologically meaningful signals or disruption of foraging behavior. We conditioned the effect of noise on the effect of prey, such that the prey variable reflects the amount of prey available in the environment, and the noise variable determines the proportion of that prey that could be available to (detected by) an individual whale under varying levels of background noise.

We do not have data to quantify the extent to which anthropogenic noise reduces the availability of prey to the beluga, but we can explore the likely impacts of more or less noise by decreasing or increasing the effective abundance of prey (both spring herring and 4T demersal fish biomass) in the model (i.e., prey available to the whale). To begin to explore the effects of changing noise levels, we tested scenarios where the prey biomass is multiplied by factors of 0.75x, 0.90x, 1.0x (management baseline), 1.1x, and 1.25x to represent effective prey abundance. The choice of a 25% reduction in foraging efficiency, due to masking and disturbance, is somewhat arbitrary, but is informed by previous findings that southern resident killer whales spend ~25% less time feeding in the presence of boats than in their absence (Lusseau et al. 2009). We considered a 25% increase in foraging efficiency to illustrate the potential benefit of ship quieting technology or stricter whale-watching regulations, under the assumption that demographic rates could have been impacted by noise-induced reductions in foraging efficiency since 1990. However, we note that when scenarios for possible future conditions of noise result in prey accessibility outside of the observed range that was used to generate the GAM for response of calf mortality, caution must be taken in interpreting such extrapolations.

A key caveat is that the demographic effects of noise and disturbance in our model can only exaggerate the demographic effects of prey limitation. The GAMs offered no statistical support for effects of prey on fecundity or adult survival (i.e., only on calf survival), so we did not model scenarios in which noise affected fecundity or adult survival. Neither did we consider any mechanism linking noise to vital rates other than through compromised foraging. We simply modelled noise effects as mediating the available prey-demography relationships in the GAM, i.e., prey-calf survival.

Contaminants

We used two different individual-based models to examine the effects of contaminants on the SLE beluga population. First, we used the model developed previously by Hall and collaborators (Hall et al. 2006; Hall et al. 2012; Hall et al. 2011) for modelling impacts of polychlorinated biphenyls (PCBs) on various marine mammal populations, but using previously published PCB loads (Lebeuf et al. 2014) and demographic rates for belugas (Table 1), as above. Additional details of the data used to estimate the dose-response function and how it is used to modify calf survival in the individual-based model are given in Hall et al. (2012) and Hall et al. (2006).

Each calf receives a portion of the PCB load of its mother through gestation and lactation, while breeding females reduces (depurates) a portion of their load of PCBs (and other persistent organic pollutants [POPs]). Except for the depuration in breeding females, PCBs continue to accumulate over time in each animal. We modelled this process of the initial PCB load in calves, depuration in breeding females, and accumulation over time in the individual-based simulations. The proportion of maternal PCBs accumulated by the fetus during gestation was set at 0.6, and a further 0.77x the maternal PCB level is transferred during lactation (as estimated from published data for other cetacean species; see Hall et al. 2006 for details). The transfer of PCBs through milk depurates the maternal PCB levels by the 0.77 proportion. It is assumed that when a calf dies during its first year, the maternal PCB load is reduced by only half as much as when the calf survives. Each individual female in the model has a state variable of alive or dead, an age and a blubber PCB concentration (determined in a model run-in). Survival and birth outcomes are determined by whether a random number (drawn from a uniform distribution between zero and one) was less than or equal to the probability associated with that event.

The simulations produced an estimate of the concentration of PCBs in the adult females between the ages of 14 and the maximum breeding age of 50 years (Figure 2). At an annual accumulation of 1 mg/kg, the mean concentration of blubber PCBs for the adult females was 5.84 mg/kg lipid weight. At 2 mg/kg annual accumulation, this increased to 12.0 mg/kg lipid weight, as shown in Figure 2. At 3 mg/kg annual accumulation the estimated concentration in adult females was 17.04 mg/kg.

Empirical data (Lebeuf et al. 2014) indicate that the concentration of total PCBs in adult female SLE belugas has declined over time. In the late 1980s, it was ~20 mg/kg lipid weight, declining to ~10 mg/kg lipid weight by the mid-2000s. This suggests that the modelled levels of PCBs would approximate the current degree of contamination in the female SLE belugas if the annual accumulation is ~2 mg/kg (see Figure 2). Historically, when inputs and concentrations in females were much higher, annual accumulations were likely to have been between ~3 and 4 mg/kg lipid weight.

The effect of maternal PCB loads on calf survival is the effect that has received the most study, and strong effects on calf survival have been reported in other cetaceans (Hall et al. 2006, 2012). We simulated the growth of the SLE beluga population incorporating the effect of the maternal load of PCBs on the probability of survival of her calf using a stochastic approach to capture the uncertainty in the model parameters and in the dose-response relationship, as shown in Figure 3.

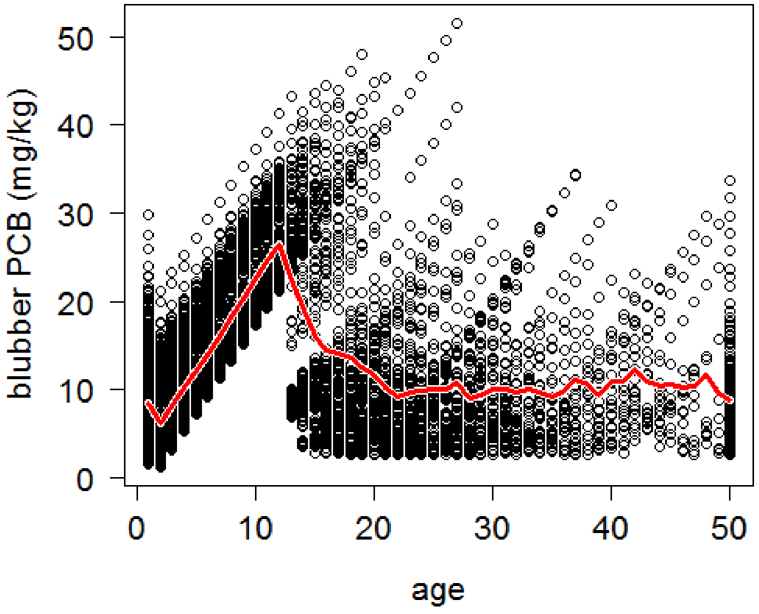

Figure 2. Estimated concentration of PCBs in females by age at an annual accumulation of 2 mg/kg lipid weight resulting in a mean concentration in the breeding age females of ~12.0 mg/kg lipid weight. Dots represent individuals in the model, red line connects the mean at each age.

Subsequently, to model contaminants in the Vortex model that we are using to project effects of other threats, we specified in the Vortex model that PCBs would accumulate in each female according to the pattern and rates similar to those described above, and that the effect of maternal PCB load on the probability of survival of each calf would be as specified in the above model. The implementation of PCB impacts in the Vortex model differed slightly from the Hall model. The initial load of PCBs transferred to the fetus during gestation will be reduced as a proportion of lipid weight as the neonate grows (a growth dilution effect). In our model of the PCB impacts on the SLE belugas, we included only the effect of maternal PCBs on calf survival. Effects on other stages of life and through other mechanisms probably exist, but we do not have quantitative data to allow us to build them into our model at this time. Therefore, the only mechanism of PCB impacts in our model is through the PCB load present in adult females. In the Vortex model, we conservatively omitted the initial load of PCBs that are accumulated *in utero*, and started each calf with a PCB level of 0.77x maternal PCB that is transferred via lactation.

The accumulated mean levels of PCBs and impacts on population growth were similar between the initial PCB model and the modified approach implemented in the Vortex model, even with the more conservative estimate of initial PCB load in calves in the Vortex model and the complexity added to the Vortex model to account also for other threats and sources of uncertainty. This confirms that our implementation of the contaminant effects in the Vortex model replicates well the models that Hall and colleagues have been using for other cetaceans.

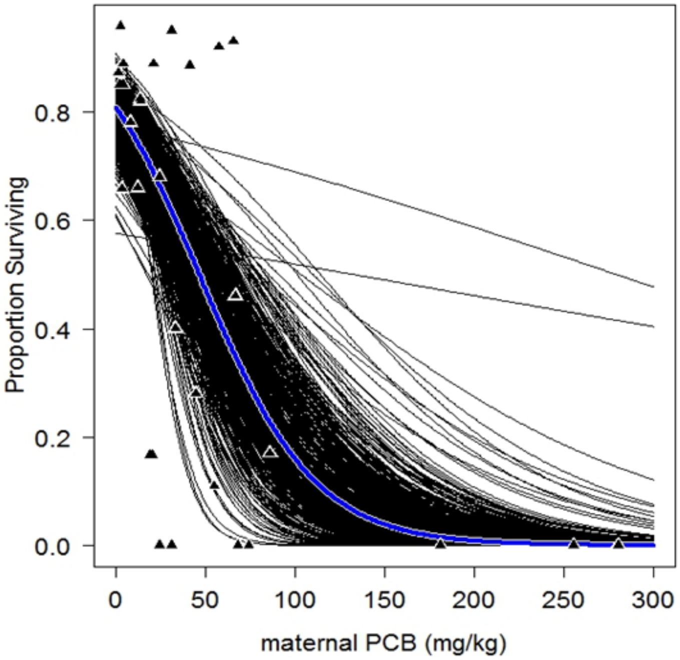

Figure 3. Combined surrogate dose-response relationship (with uncertainty) relating maternal tissue PCB concentrations to kit survival in mink used in the IBM model simulations for estimating the effects of PCBs on the potential population growth rate of SLE beluga.

Impacts of PCBs on calf survival in the model were scaled such that calf mortality at the current mean level of PCBs (achieved with an accumulation rate of 2 mg/kg lipid weight / year; see above) was set at the mortality rate expected from the GAM of SST, ICE, HER, and DEM, so that the addition of average PCB effects to our models did not shift the mean demographic rates. At other levels of PCBs that were explored in model scenarios, the calf mortality predicted from the GAM was adjusted upward or downward by the proportional change in mortality expected for those higher or lower PCB levels. This allows testing of the projected effects of contaminant levels either increasing or decreasing in the future. In the Vortex model of threats, we examined the effects of PCB accumulation rates that varied from 0 to 4 mg/kg lipid weight / year. When we tested possible future levels of PCB accumulation, we started the simulations with PCB levels at estimated current levels, rather than assuming that the PCB load in the current population was instantly changed. Therefore, the rates of PCB accumulation tested will lead to gradual changes in the levels in the belugas over the years in the model (as would occur also in the SLE population if contaminant levels change in the environment) as initial animals are replaced by recruits and breeding females depurate their prior PCB load.

Importantly, the models used here predict demographic consequences only of PCBs, because dose-response curves are not available for other contaminants of relevance to SLE belugas (e.g., polybrominated diphenyl ethers, “PBDEs”). Information is available on lethality or morbidity due to oral intake of various chemicals in laboratory studies, but the PVA model requires information on demographic (or health) effects in the field of metabolism of contaminants stored in blubber, because this is what is available most often from biopsy studies.

PCBs are not the only persistent organic pollutants (POPs) that affect the beluga (Lebeuf et al. 2014). Lacking data on the effects of other POPs, the effects of PCBs in the population model can be considered to represent the suite of contaminants in the system. That is, by projecting effects of increased or decreased levels of PCBs, we can represent the expected consequences of reductions in POPs generally. Obviously, this representation will be at best crude if some POPs change in abundance at very different rates, or if their toxic effects and dose-response curves differ from that of PCBs. We do not have the data that would allow us to more accurately scale impacts of other POPs to the modelled changes in PCBs.

Harmful algal blooms

There is some evidence to suggest that harmful algal blooms (HABs) can affect mortality of the SLE belugas, either due to direct toxicity or secondary impacts through depletion of prey abundance (Scarratt et al. 2014). Such events could be damaging to the beluga population because the slow potential population growth could cause reduction in the population size for many years after an event. These kinds of uncommon and unpredictable events can be modelled in Vortex as “catastrophes” – with specified probability of occurrence and severity of effects on reproduction and survival. To the extent that HABs were a cause of the mean and variation in demographic rates observed since 1990, their impacts would already be included in our models. However, predicted changes in the frequency or severity of HABs could be modelled if their effects were separated out from the background demographic rates. We included a catastrophe process in the Management Scenarios (see below) to allow modelling of future increases in the frequency or consequences of catastrophes, which could include HABs, oil spills, or an epidemic arising from a novel pathogen that SLE belugas did not experience since 1990. For now, the frequency and consequences of catastrophes are both set to 0, because any effects of HABs since 1990 are already subsumed within the demographic rates we used in the PVA.

SCENARIOS

Initial population model

An initial population model was run using the demographic rates shown in Table 1. This initial model used estimated average rates for the SLE beluga over recent decades, with variation over time and uncertainty expressed as distributions of parameter estimates. The uncertainties in the rates were entered into the model by sampling each rate for each iteration from the distribution describing its uncertainty. This model was then used to examine the influence of these uncertainties on the projected population growth. Thus, changes over time in environmental conditions and threats experienced by the population would be encompassed by the distribution of population projections produced by the model, but were not explicitly modelled as separate causal factors determining the demographic rates.

Time period regimes

During the years of intensive data collection on environmental variables (1990 – 2012), several distinct periods or regimes of population performance have been noted. From 1990-1999, a period that can be described as the “Past” regime, SST was lower, ice duration longer, and herring biomass greater than in more recent years (Table 2). From 2000 through 2012, a period that can be described as the “Present” regime, SST was higher, ice duration shorter, and herring biomass much lower than previously (see also Plourde et al. 2014). These trends continued to increase in the most recent years, and the period 2008-2012 might best represent the regime under current climate change scenarios (Loder et al. 2013). We therefore examined three climate change regimes (each using the 2000-2012 levels of prey): “Climate-SST” projects future SST to be as observed since 2008; “Climate-ICE” projects future ice to be as observed since 2008; “Climate-SST+ICE” projects both environmental conditions to remain at 2008-2012 levels.

Table 2. Means and SDs of the environmental and prey variables during each regime. Demersal means exclude years 1993 and 2003. Data provided by DFO. For prey, the re-scaled index relative to the maximum prey biomass observed since 1990 is given in parentheses.

Regime	SST mean	SST SD	Ice duration	Ice SD	Herring mean	Herring SD	Demersal mean	Demersal SD
Past (1990-1999)	9.87	0.83	104.63	8.11	80187 (0.684)	19997 (0.180)	2796 (0.529)	1469 (0.278)
Present (2000-2012)	10.52	0.74	81.52	19.16	20944 (0.179)	9921 (0.088)	2766 (0.523)	914 (0.173)
Climate-SST	11.10 (2008-2012)	0.64	81.52	19.16				
Climate-ICE	10.52	0.74	73.40 (2008-2012)	25.21				
Climate-SST+ICE	11.10 (2008-2012)	0.64	73.40 (2008-2012)	25.21				

Management scenarios

To test the effects of possible management actions affecting prey and other threats amenable to management, or otherwise changing threat levels, we built future management scenarios while including in each of them the SST and sea ice conditions from the 2008-2012 period, given that extremes observed during this period correspond to the predicted SST (and ice cover) at the end of the present century (Loder et al. 2013). For our “Management Baseline” scenario to be used as a reference against which to compare future possibilities, we therefore used the “Climate-SST+ICE” regime described above, with the prey biomasses as reported for the 2000-2012 period.

We then examined population trajectories predicted under various possible management scenarios (Table 3). In three “Prey management” scenarios, we used the prey biomasses from the 1990-1999 Past regime for HER, DEM prey, or both to test for effects of a hypothetical future increase in prey biomass following managerial actions by DFO. In four sets of “Single threat models”, we varied each of HER, DEM biomass, noise impacts on prey accessibility, and PCB accumulation rate across several levels spanning a wide range of values. For DEM and HER models, we tested biomasses that ranged from the lowest to the highest levels reported from 1990 to 2012. For Noise models, we tested impacts on the accessibility of prey that ranged from 0.75x to 1.25x. For PCB models, we tested rates of accumulation that varied from 0 to 4 mg / kg lipid / y. (See descriptions, above, of the models of each threat.) In four "Multi-threat models" we tested some combinations of two or more of the threats being improved simultaneously to the best conditions tested in the single-threat models.

Table 3. Scenarios used for projecting fates of the SLE beluga population under various possible management changes to prey biomass, noise impacts on prey accessibility, and PCB contamination.

Management baseline

Scenario	Herring (mean relative index)	Demersal (mean relative index)	Noise (impact on prey accessibility)	PCB (accumulation rate; mg/kg/y)
Management baseline	0.179 (2000-2012)	0.523 (2000-2012)	1x	2

Prey management

Scenario	Herring (mean relative index)	Demersal (mean relative index)	Noise (impact on prey accessibility)	PCB (accumulation rate; mg/kg/y)
Prey-HER	0.684 (1990-1999)	0.523 (2000-2012)	1x	2
Prey-DEM	0.179 (2000-2012)	0.529 (1990-1999)	1x	2
Prey-DEM+HER	0.684 (1990-1999)	0.529 (1990-1999)	1x	2

Single threat models

Scenario	Herring (mean relative index)	Demersal (mean relative index)	Noise (impact on prey accessibility)	PCB (accumulation rate; mg/kg/y)
Demersal fish	0.179	0.2 to 1.0	1x	2
Herring	0.1 to 1.0	0.523	1x	2
Noise	0.179	0.523	0.75x to 1.25x	2
PCB	0.179	0.523	1x	0 to 4

Multi-threat models

Scenario	Herring (mean relative index)	Demersal (mean relative index)	Noise (impact on prey accessibility)	PCB (accumulation rate; mg/kg/y)
Reduced Noise + no PCBs	0.179	0.523	1.25x	0
Maximum Prey	1.0	1.0	1x	2
Max. Prey + no PCBs	1.0	1.0	1x	0
Max. Prey + no PCBs + reduced Noise	1.0	1.0	1.25x	0

Finally, we ran a model in which all of the threats were varied simultaneously among the iterations of the simulation, by sampling each threat factor from a uniform distribution across the range tested in the single-threat models. Statistical analysis of the effect of each threat factor on the population growth was used to indicate how much each threat drives the fate of the SLE population, given the ranges of threats that we examined. The Vortex model can be used for testing other hypothesized or predicted future conditions or management scenarios, and the Vortex input file used for all analyses presented in this report is available.

RESULTS

INITIAL POPULATION MODEL

Figure 4 shows the mean trajectory (± 1 SD) for the initial population model run with input demographic parameters and ranges set as described in Table 1, with no additional impacts of SST, ice, prey, noise, or contaminants. The mean population growth rate projected from the long-term average demographic rates is marginally positive, with r = 0.0002. There is considerable uncertainty in the trajectory, with SD(r) = 0.0203 for the variation in growth across years and across iterations that sampled demographic rates from the uncertainties in estimates of those rates. None of the simulations predicted extinction within 100 years, but the confidence intervals around predicted population size are wide.

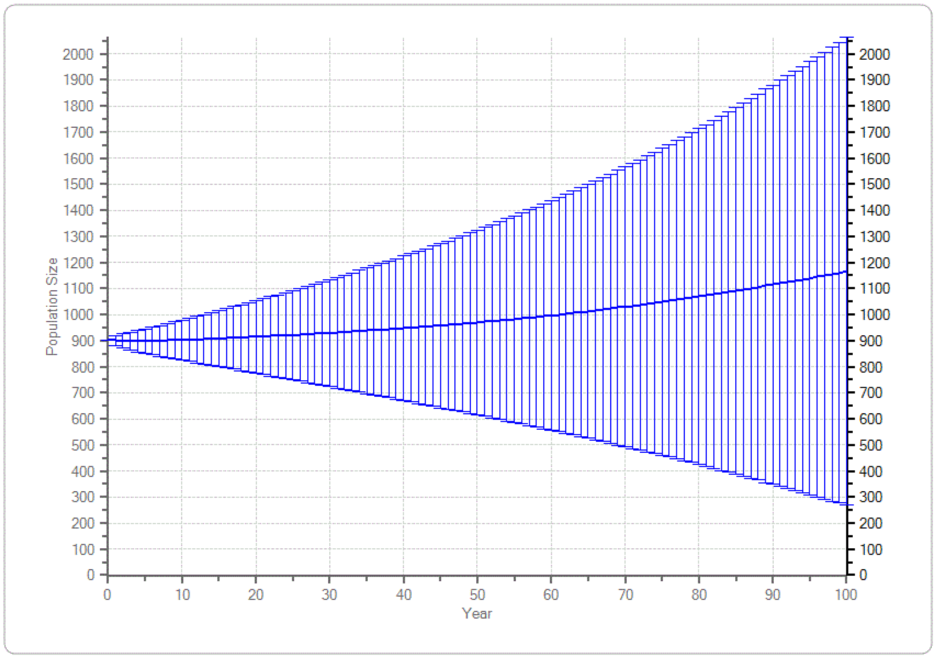

Figure 4. Mean population size (with SD across iterations) from 10,000 iterations of the baseline model, with demographic rates given in Table 1.

To further illustrate the uncertainty in trajectories over time and among iterations, the next graph displays 100 sample iterations of this initial model.

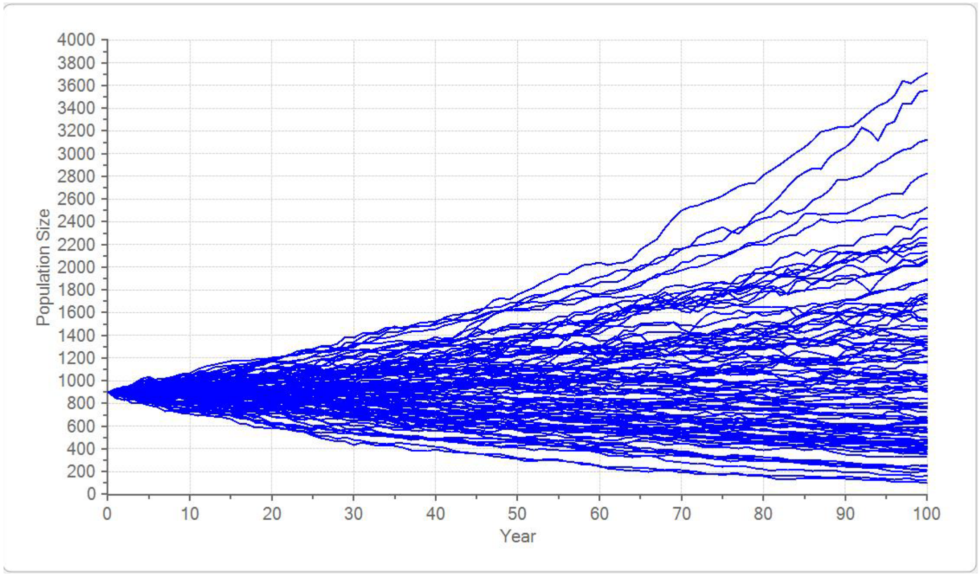

Figure 5. A typical set of 100 PVA projections of the SLE beluga population under long-term demographic rates, given the levels of uncertainty in each parameter as listed in Table 1, and the inherent unpredictability of demographic processes.

Across the ranges of values that we tested for each parameter sampled in 10,000 iterations of the simulation, the proportion of variance in the population growth rate (r) that was accounted for by the sampled variation in each parameter is given in Table 4.

Table 4. Proportion of variance in the population growth rate (r) across iterations that was accounted for by the sampled variation in each demographic parameter. The range tested was sampled from a normal distribution for the first three variables and from a uniform distribution for the last two. The residual variance is due to the inherent unpredictability of population demographic processes.

Demographic Parameter	**Mean**	**Range tested**	**Proportion of variance**
Fecundity	0.326	SD = 0.023	0.189
Calf mortality	0.237	SD = 0.041	0.110
Adult mortality	0.061	SD = 0.0055	0.633
Environmental Variation-Fecundity	0.06	0.00 to 0.12	0.000
EV-Calf Mortality	0.06	0.00 to 0.12	0.000
Residual			0.065

Uncertainty in the adult mortality had the largest impact on uncertainty in the population growth rate (63.3% of variance), with fecundity (18.9%) and calf mortality (11.0%) having lesser but still noticeable influence. Annual variation in fecundity and calf survival (EVs) appear unimportant to the long-term population trajectory, except if larger fluctuations result also in depressed mean fecundity or mortality rates. The Residual variance due to uncertainty in demographic processes that arises from random variation in the fates of individuals (demographic stochasticity) contributed relatively little to variation in population growth, as expected for a low-fecundity, long-lived species.

TIME PERIOD REGIMES

Figure 6 compares the mean trajectories projected under regimes representing the environmental and prey conditions during different time periods. Under the “Past” conditions from 1990-1999, mean population growth would be marginally positive (r = 0.001), but with large uncertainty that includes the possibility of population decline (SD(r) = 0.022; Figure 7A). Under the “Present” conditions experienced since 2000, mean population growth is projected to be slightly negative, but with a range of projections that includes the possibility of growth (r = -0.007, SD = 0.026; Figure 7B). If Ice duration is projected to be lower as it was in 2008-2012, then population decline is faster (r = -0.012, SD = 0.030). If SST remains elevated as it was in 2008-2012, the impact on population growth (r = -0.013, SD = 0.028) is similar to the impact of the reduced Ice. The scenario that will be used to test management options (“Climate-Ice+SST”), with recent sea temperature and ice conditions as in the recent years (2008-2012), but prey biomasses typical of the 2000-2012 period, projects a decline (r = -0.019, SD = 0.032).

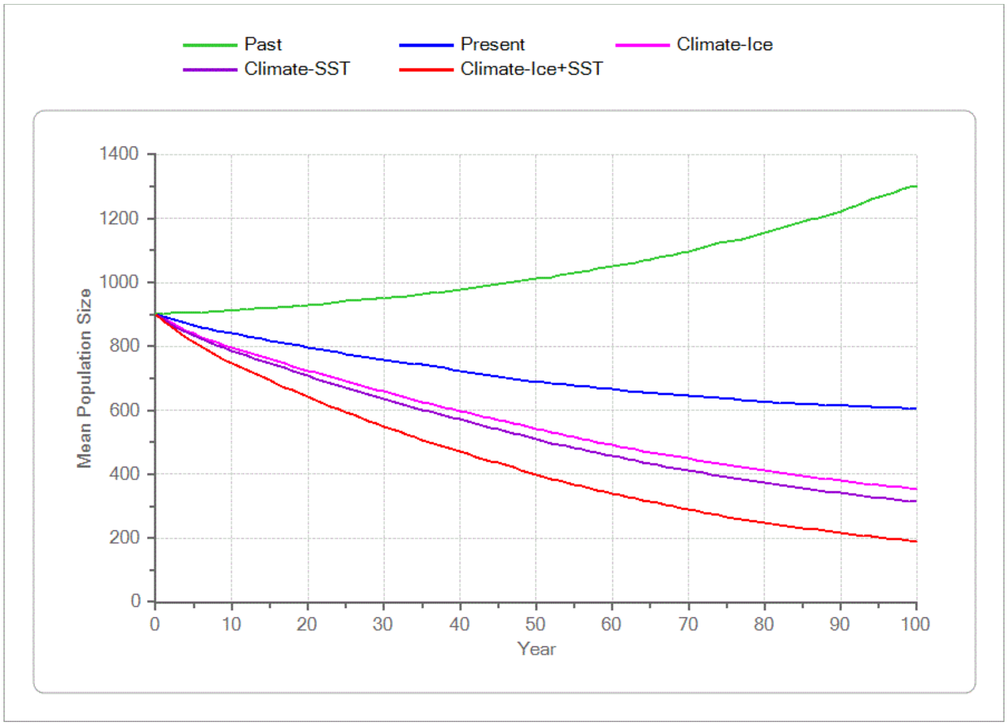

Figure 6. Mean projected population sizes under regimes representing conditions in different time periods: "Past" (1990-1999); "Present" (2000-2012); Climate-Ice (2008-2012 Ice, with 2000-2012 SST and prey); Climate-SST (2008-2012 SST, with 2000-2012 Ice and prey); and Climate-Ice+SST (2008-2012 Ice and SST, with 2000-2012 prey).

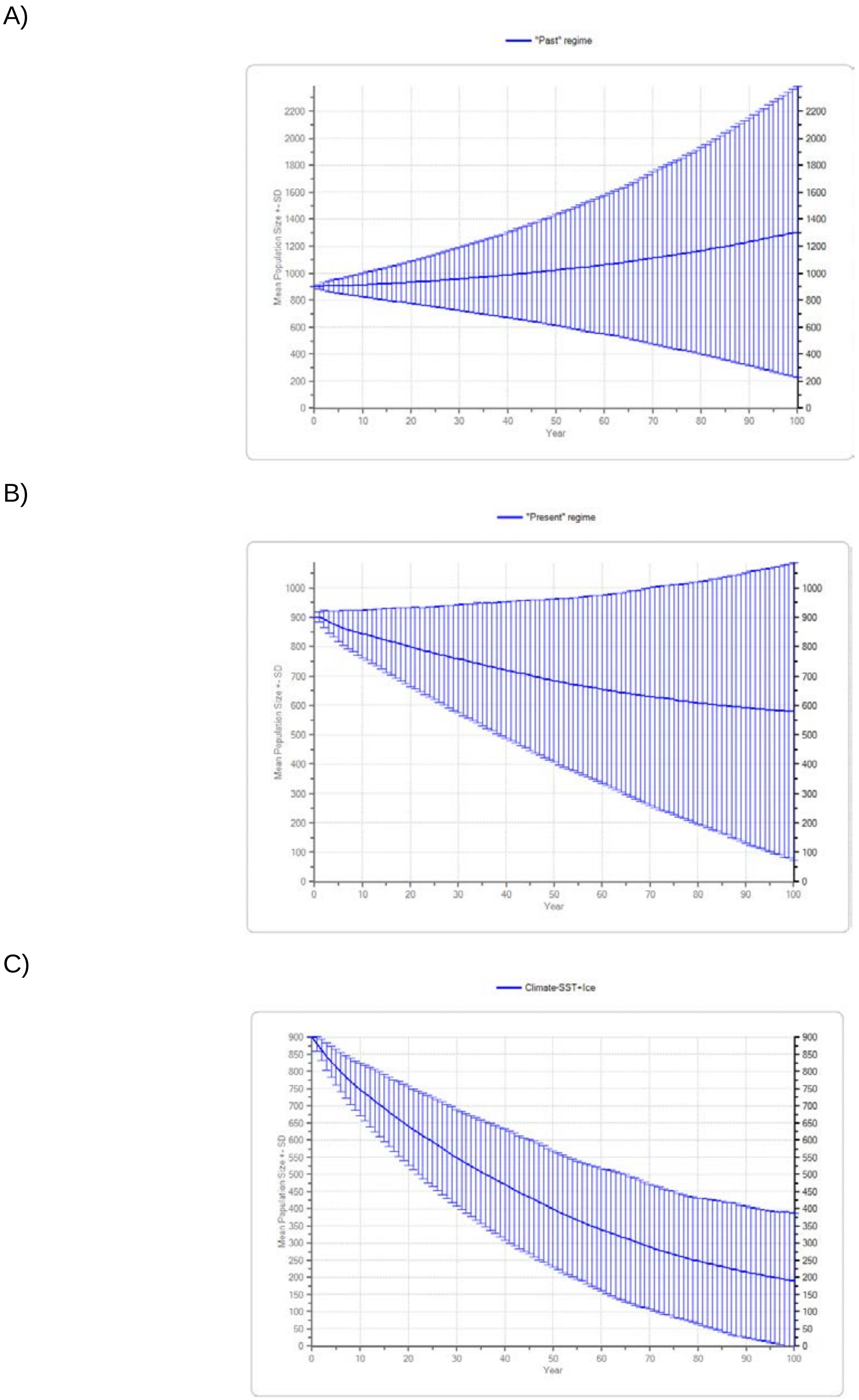

Figure 7. Mean population sizes, with error bars showing 1 SD across iterations, projected for three regimes representing conditions during different time periods: (A) "Past" (1990-1999); (B) "Present" (2000-2012); and (C) "Climate-SST+Ice" (climate conditions from 2008-2012).

PREY MANAGEMENT SCENARIOS

The mean population trajectories predicted from the scenarios that test improvements in HER, DEM, or both prey biomasses to the levels observed in 1990-1999 are shown in Figure 8. This change to DEM biomass has almost no effect on the population projections, because the mean DEM biomass was almost the same in 1990-1999 and 2000-2012 (Table 2). However, there were large fluctuations in DEM biomass within each of these time periods, and DEM biomass does significantly influence calf mortality (Appendix 1), so there might be scope for management improvements to DEM biomass that would have beneficial effects on the SLE belugas (e.g., see Figure 10, below). Changing the DEM biomass to the 1990-1999 levels decreased population growth slightly relative to the Management Baseline, because the larger annual variation in demersal in the earlier decade leads to more years in the simulation in which a lack of DEM prey reduces calf mortality. (Improvements to the DEM biomass much above mean levels have little benefit, because of the assumed threshold effect; see Figure 1.)

Herring biomass was almost 4-fold higher in 1990-1999 than subsequently. If HER biomasses are returned to the higher levels reported in the 1990s, the population growth rate is projected to increase to r = -0.013 from the r = -0.019 in the Management Baseline.

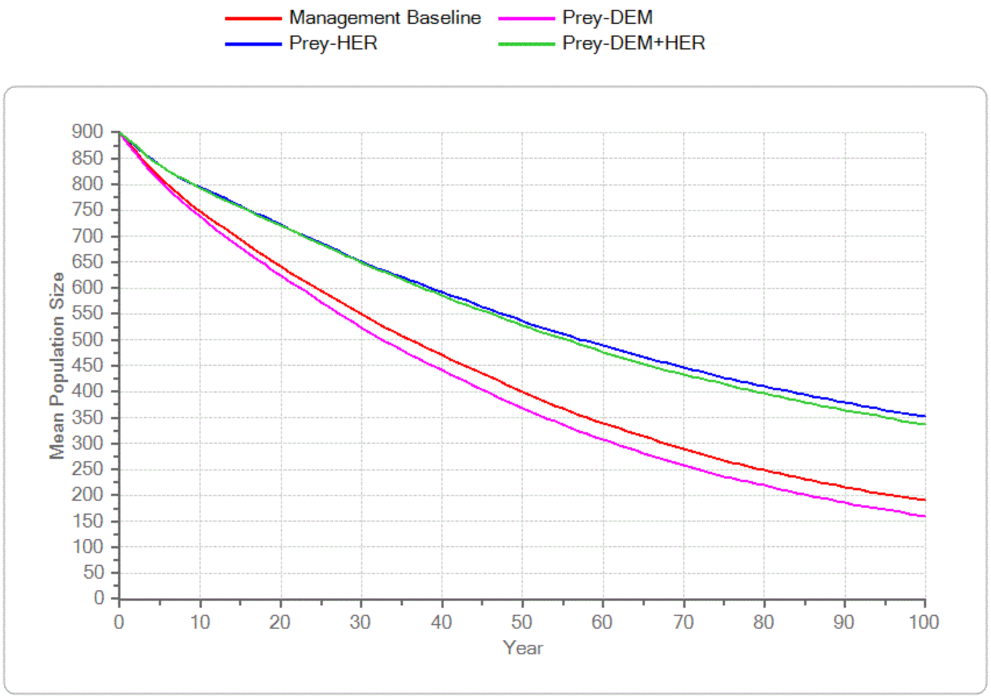

Figure 8. Mean population sizes projected under scenarios of Herring (“Prey-HER”), Demersal (“Prey-DEM”), or both (“Prey-DEM+HER”) biomasses returned to the levels reported in 1990-1990. These scenarios assume SST/Ice conditions in the range of those observed for the period 2008-2012.

SINGLE THREAT MANAGEMENT SCENARIOS

In each of the sub-sections, below, comparing possible alternative levels of threats (Figures 9, 10, 11, and 14), the “Management Baseline” conditions are compared to a few scenarios that are more optimistic or pessimistic. The most optimistic line in each case represents a “best case” management scenario, with the maximum prey level observed in recent decades (for Herring and Demersal scenarios), no PCB accumulation from the environment (for the PCB scenarios), or reduction in noise disturbance sufficient to allow 25% more prey to be available to the belugas (for Noise scenarios).

Prey

Figures 9 and 10 compare the mean population trajectories for various levels of HER and DEM biomass, respectively, that span the range observed since 1990. Across the range of prey biomasses observed since 1990 (0.1 to 1.0 relative index for Herring; 0.2 to 1.0 relative index for DEM), the beluga population is projected to decline even if prey return to the highest levels observed. This prediction occurs because these models include impacts of generally lower Ice and greater SST since 2008. With the predictions from the GAM, the benefit of more DEM biomass plateaus above an index of about 0.6 relative to the maximum value (Figure 10). Thus, it might be that HER biomass would need to reach levels beyond the range for which we have data to estimate impacts (or other management actions would be needed) in order to achieve population growth. Whether further increases in HER biomass above the observed range would be beneficial to belugas is not known.

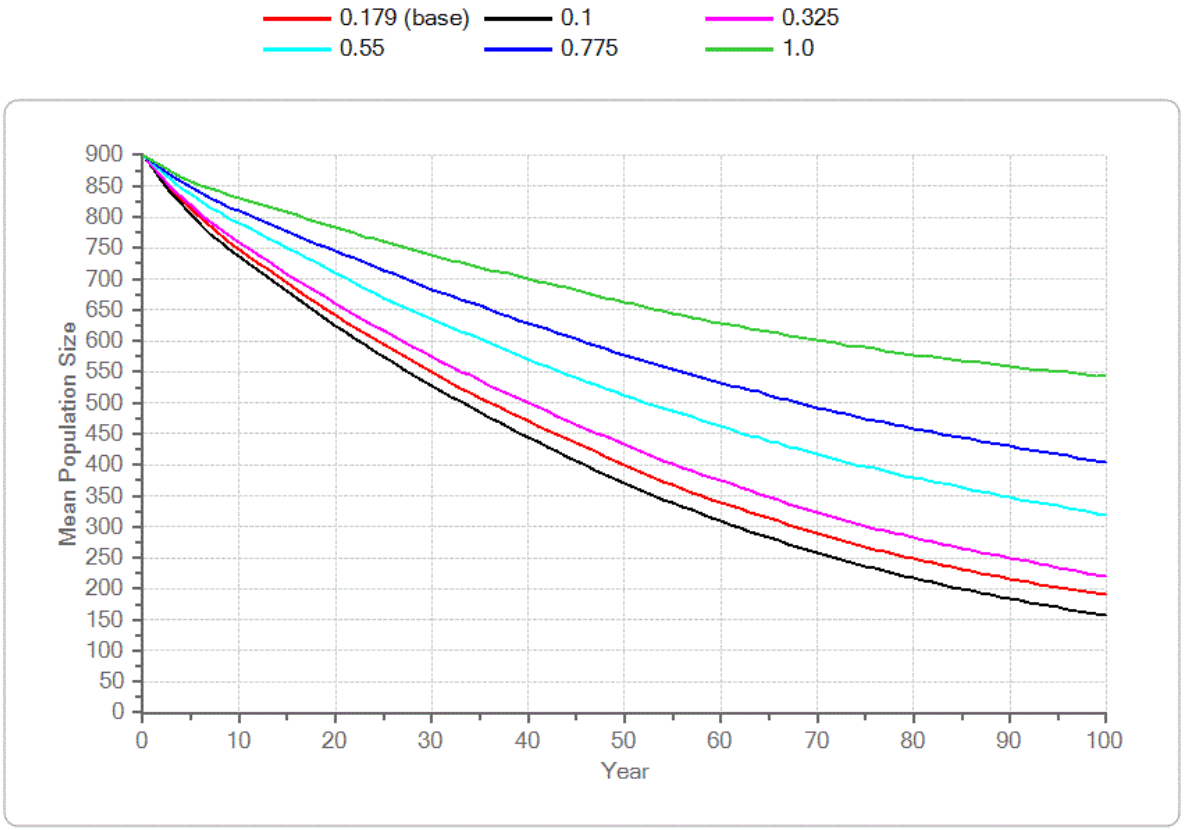

Figure 9. Mean population sizes projected under several levels of herring biomass that range from the lowest (relative index = 0.1) to highest (1.0) seen since 1990. The "Baseline" scenario (red line) applies the mean herring biomass from 2000-2012. These scenarios assume SST and Ice conditions as observed for the period 2008-2012.

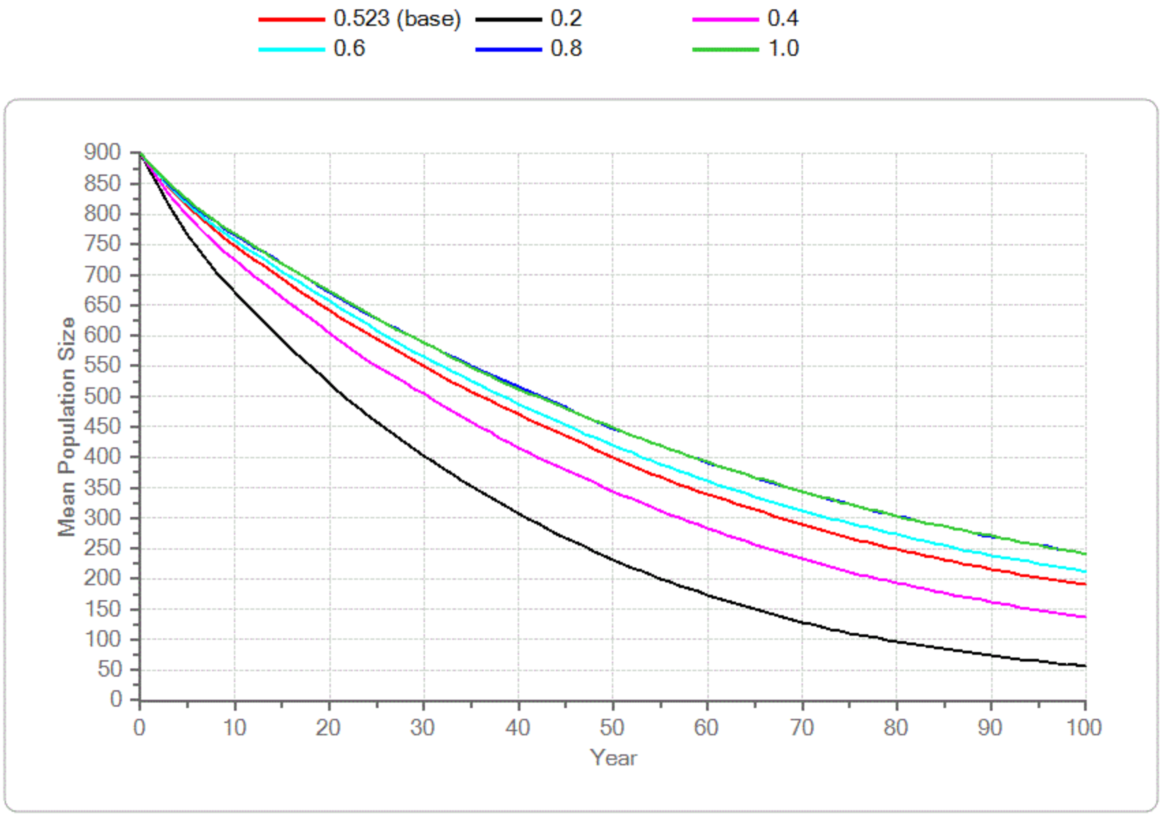

Figure 10. Mean population sizes projected under several levels of demersal fish biomass that range from the lowest (relative index 0.2) to highest (1.0) seen since 1990. Lines for the highest levels are superimposed because the benefit of more demersal prey plateaus. The "Baseline" scenario (red line) applies the mean demersal fish biomass from 2000-2012. These scenarios assume SST and Ice conditions as observed for the period 2008-2012.

Noise

High noise levels might reduce the window of time during, or the area over, which the belugas can forage effectively. Figure 11 shows the mean population trajectories under a range of noise conditions, acting in the model as modifiers of prey levels, which in turn modify calf mortality. Over the range tested (i.e., a 25% increase or decrease in effective prey availability to the belugas), the shifts in the mean population trajectories caused by noise are less dramatic than those shown above for tests of prey levels (Figures 9 and 10). An advantage to treating the prey biomass and the noise levels as independent factors entered into the model is that the individual and cumulative effects of proposed management scenarios that include prey enhancement and/or noise reduction will be more transparent. It is also possible that quantification of other effects of noise that do not translate through the effective availability of prey will be considered in future models.

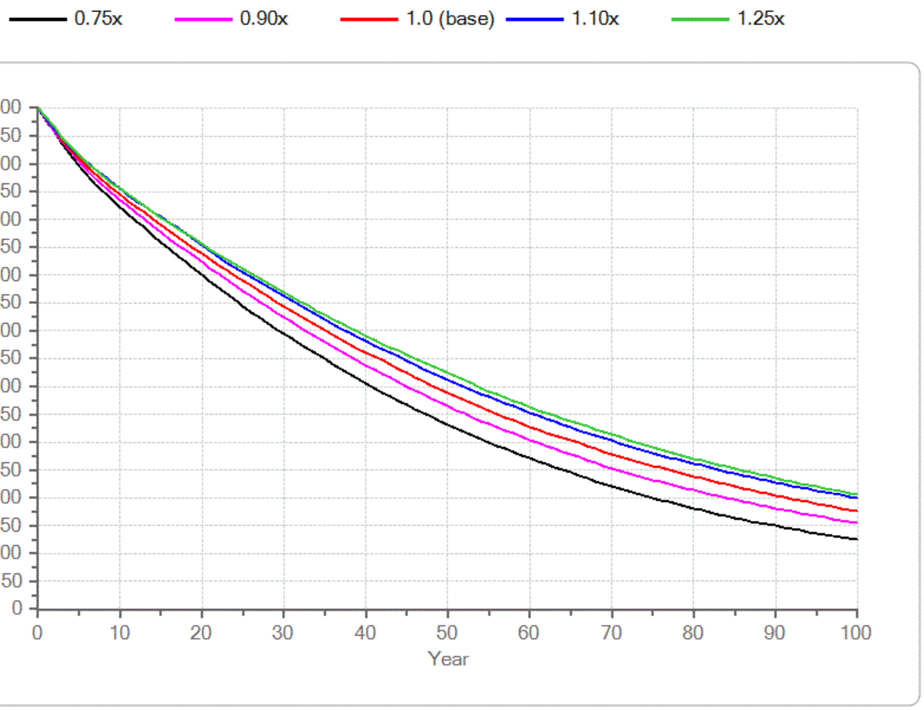

Figure 11. Predicted mean population trajectories under several levels of noise conditions that impede effective foraging. The effect of noise was modelled as a change in the available prey, ranging from a reduction of 25% in availability (noise factor 0.75x) under high noise conditions to an increase of 25% (1.25x) if noise is reduced from current levels such that feeding is much less impeded by noise disturbance. The “1.0” line is the management baseline with no adjustment of prey availability.

Contaminants

PCB impacts assessed with the model presented in Hall et al. (2006, 2012)

The initial model of PCB impacts, using the approach of Hall et al. (2006, 2012), focused on quantifying the reduction in population growth rate in order to determine what exposure levels would affect population growth or even cause population decline. Using the estimated mean population parameters from Table 1 to set up an initial population with a stable age structure, this model gave a population with an annual growth rate of ~0.6% (r = 0.006), which is in line with the growth estimated under the long-term average demographic rates. For comparison, the replication in Vortex yields an initial scenario with mean r = 0.0002. The confidence intervals on these estimates overlap.

The results for the 100 replicates of 100-year simulations with an annual accumulation of between 1 and 7 mg/kg PCBs are shown in Fig. 12. This plot shows the mean population growth for the set of simulations, the 95% confidence limits, and the 2.5 and 97.5 percentiles of the modelled population trajectories. At the highest annual accumulation level, the mean estimated potential population growth between years 65 and 90 was reduced very slightly by ~0.8% but this resulted in a mean population trajectory that is declining rather than being stable (Figure 13). However, it should be noted that there is considerable uncertainty associated with these conclusions, with the confidence intervals ranging from population growth rate (λ) < 1 to λ > 1 at each annual accumulation level (Figure 12).

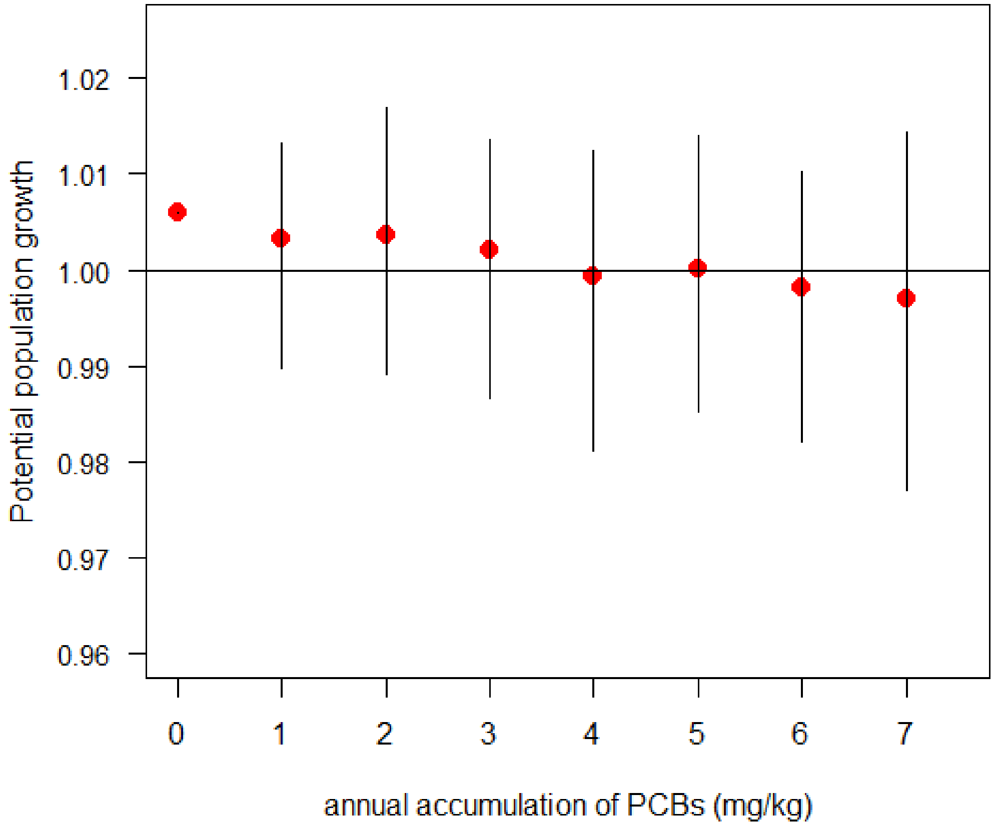

Figure 12. Hall et al. (2006, 2012) model. Change in potential population growth with different PCB annual accumulation concentrations (mean and 95% confidence intervals) in model simulations with effects of PCBs on calf survival only. All other demographic rates are as given in Table 1, representing the long-term conditions (rather than the Management Baseline or other models of recent time period regimes. These simulations only model uncertainty in the PCB effects, and ignore demographic stochasticity. As a result, there is no variability in lambda when PCB is set to 0.

The population trajectories from the model output at the highest PCB exposure modelled are shown in Figure 13. However, as can be seen in Figure 12 at lower accumulation levels, less than ~6 mg/kg per year, the model outputs suggest that with the overall demographic rates the population is likely to remain stable.

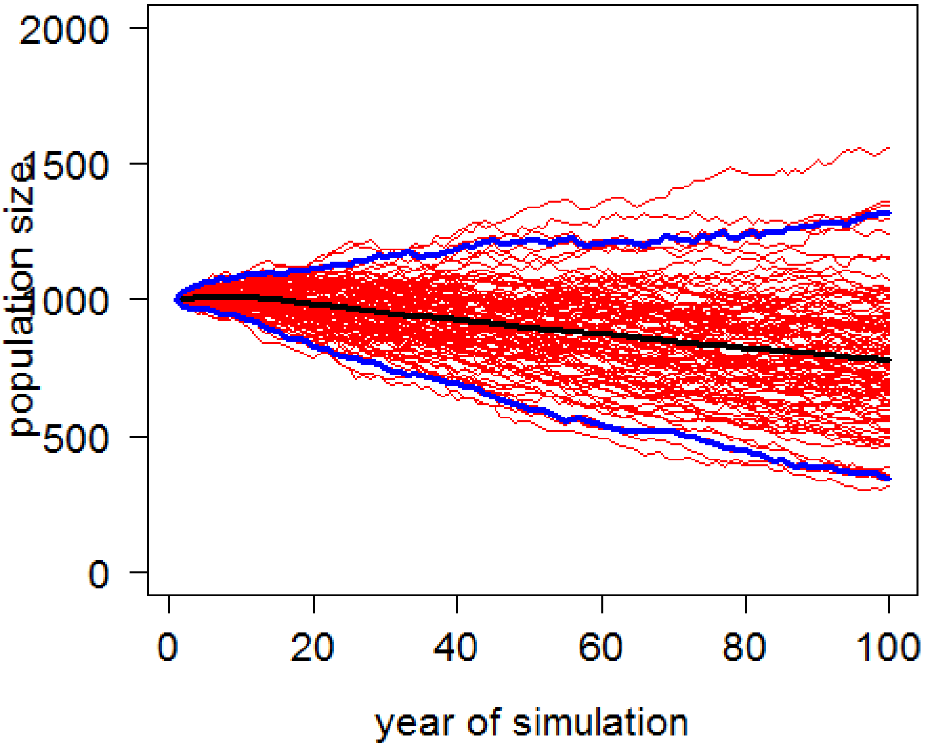

Figure 13. Hall model. Population trajectories for simulated SLE beluga exposed to PCBs at an annual accumulation level of 7 mg/kg lipid weight.

These initial model simulations suggest that if PCBs were only affecting offspring survival, the SLE beluga would not be substantially affected at the population level. However, PCBs have additional adverse health effects, particularly on immune functions. Any pathogens that are already circulating in the population would be accounted for in the underlying causes of natural mortality reported in existing demographic rates, but novel or increased levels of pathogens could have additional impacts on a population exposed to PCBs. The model has been further developed to allow modelling of any such additional effects. However, an estimate of the proportion of the population exposed to a novel pathogen would have to be estimated for additional simulations.

PCB impacts assessed in the Vortex model

The Vortex model with varying PCB accumulation rates applied to our Management Baseline projects lower population growth rates than the Hall model above, with mean r = -0.016 to -0.024 for PCB accumulation rates of 0 to 4 ppm in the Vortex model compared to growth from about r = 0.006 to about r = 0.000 in the Hall et al. model at these rates. This difference between models occurs because the Vortex model imposed the PCB effects on the scenario with environmental conditions (SST and Ice) from recent years and projected for the future, whereas the Hall et al. model was run using beluga demography parameters from Table 1. The relative shift in growth rate was similar in the two models, and the Vortex model confirms the results from Hall et al. that show that PCBs can depress population growth, but by lesser amounts than other threats.

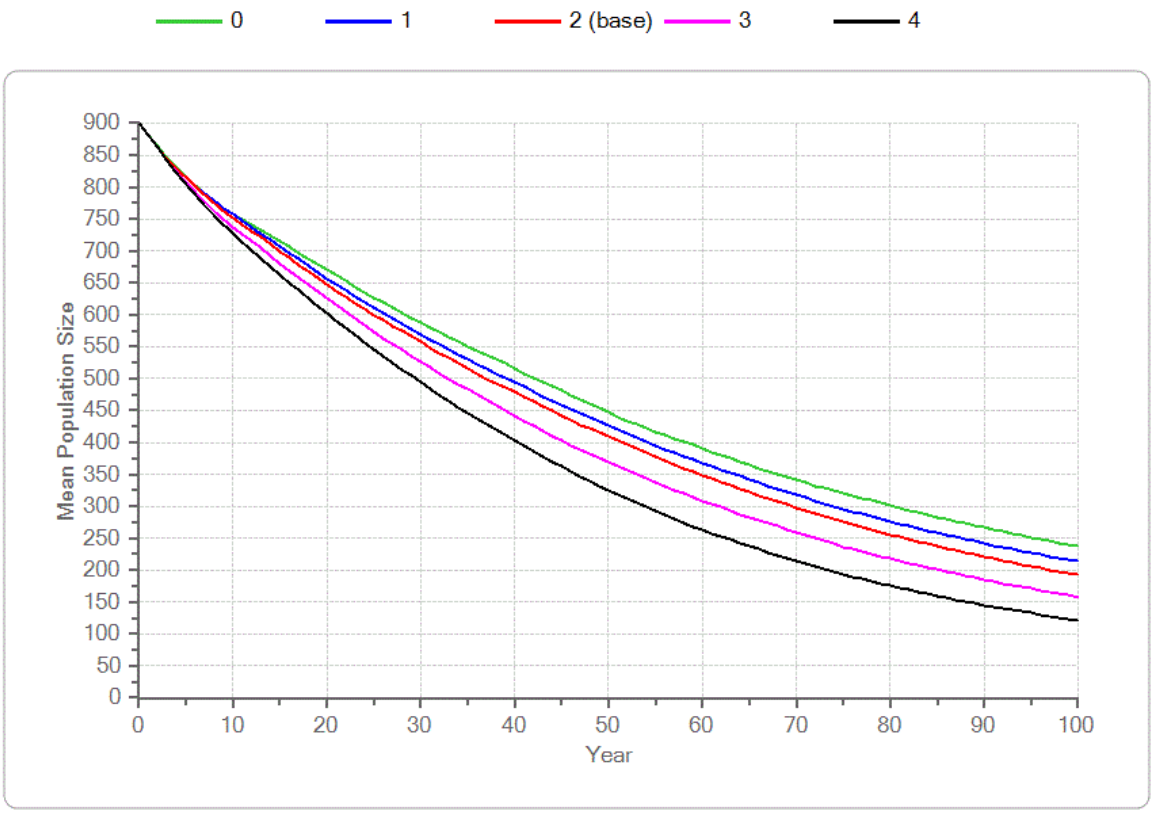

Figure 14. Mean population sizes projected under several rates of PCB accumulation (0, 1, 2, 3, and 4 ppm / year). The "2" line is the management baseline model with current levels of PCBs.

MULTI-THREAT MANAGEMENT SCENARIOS

The analyses presented above indicate that amelioration of any one threat, within ranges that seem feasible to change, are not sufficient to achieve reliable positive population growth. This occurs because the management scenarios presented above are not sufficient to overcome the predicted negative impacts of warming sea temperatures and decreased ice (Figure 6). Therefore, we tested scenarios in which improvements were made to the several threats in combination (Figure 15).

To achieve consistent positive population growth in the model, *all* threat reductions – actions toward restoring prey biomass, increasing feeding efficiency via reduction in noise disturbance, and removing PCBs from the environment – would be required (Figure 15). Even under this most optimistic scenario, the population is projected to grow only 0.3% per year. This occurs because the higher SST and low ice duration are predicted to continue to depress calf survival. Just the increase in prey biomass coupled with removal of PCBs ("Max. prey, no PCB") also will allow eventual return to positive population growth, but not until the PCB loads in the existing animals are eliminated through depuration and population turn-over.

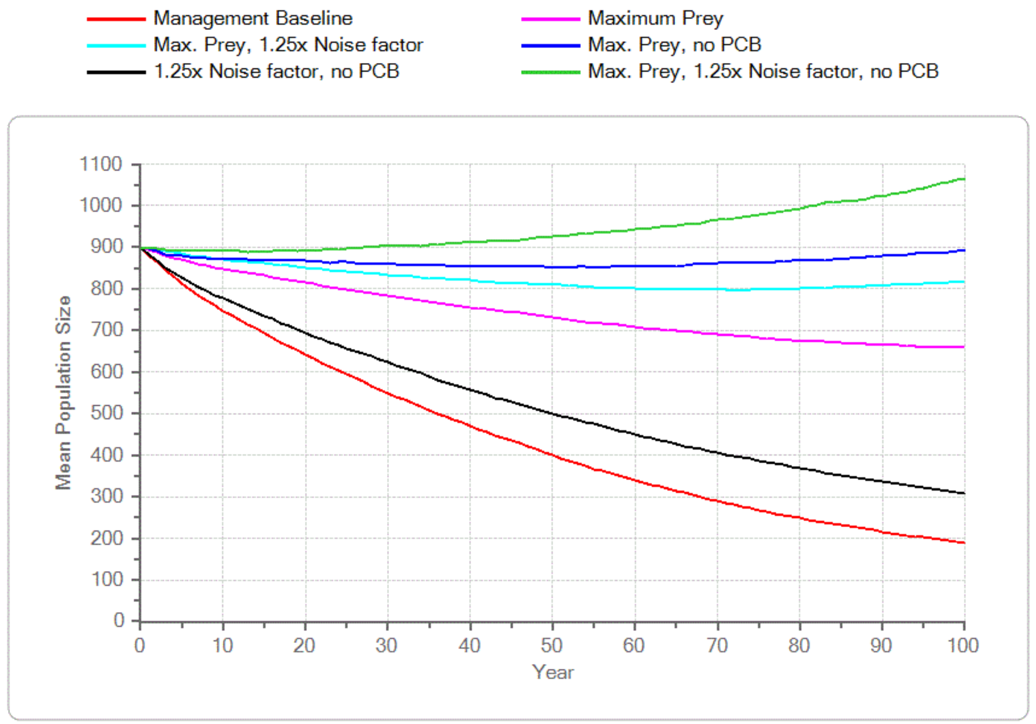

Figure 15. Mean population sizes projected if the current environmental conditions (period 2008-2012) and recent prey biomasses (2000-2012) persist ("Management baseline"), both 4T herring and demersal fish biomass are restored to the highest levels observed in recent decades ("Maximum prey"), prey are restored to the highest levels observed and noise is reduced so that prey availability is increased 1.25x ("Max. prey, 1.25x noise factor"), noise is reduced and PCB contaminants in the system are eliminated ("1.25x noise factor, no PCB"), prey are restored to the highest levels observed and PCB contaminants are eliminated ("Max. prey, no PCB"), or all threat reductions are achieved as noise is reduced so that prey availability is increased 1.25x, the highest levels of prey are restored, and PCB contaminants are eliminated ("Max. prey, 1.25x noise factor, no PCB").

COMPARING THREATS IN A COMPREHENSIVE MODEL

The impacts of varying levels of HER, DEM, noise, and PCBs were put into a common model that sampled climatic variables (SST and Ice) from distributions with their recent (2008-2012) means and SDs. Replicating the ranges used in tests of individual threats above, the two prey biomass variables were sampled from uniform distributions from the minimum to the maximum values observed since 1990, the noise factor applied to prey was sampled from a uniform distribution from 0.75 to 1.25, and the rate of PCB accumulation was sampled from a uniform distribution from 0 to 4 ppm / year. The cumulative effects model with all the threats varied was repeated for 10,000 iterations to generate precise data on the relative value of management actions that might address each threat.

Table 5. Proportion of variance in the population growth rate (r) across iterations that was accounted for by the sampled ranges for demographic rates and for each threat. The summed variance proportions for the two demographic rates and for the four threats are shown in bold. The residual variance is due to the uncertainty in the relationships of input variables (SST, ICE, HER, DEM, noise, and PCB) to calf mortality, as well as the inherent unpredictability of population demographic processes.

	Mean	**Range tested**	**Proportion of variance**
Demographic parameter			**0.408**
Fecundity	0.326	SD = 0.023	0.090
Adult mortality	0.061	SD = 0.0055	0.318
Threat (affecting calf mortality)			**0.327**
Herring	0.55	0.1 to 1.0	0.121
Demersal fish	0.60	0.2 to 1.0	0.123
Noise	1.0	0.75x to 1.25x	0.034
PCB	2	0 to 4	0.049
Residual			0.265

The relative importance of the factors in the model across a given range of values can still provide a useful guide as to where management emphasis might be focused. With the ranges tested for key demographic rates (fecundity and adult mortality) and for the threats that influence calf mortality in the model, the uncertainties in the demographic rates account for 41% of the total variation in projected population growth in the model, while the threats account for 33%. The uncertainty in functional relationships of the variables included in the GAM and PCBs to calf mortality account for most of the remaining 26% of the variation, and inherent demographic stochasticity would contribute a small amount to this residual variation.

As was seen in the exploration of parameter uncertainty in the initial model (Table 4), adult mortality was a greater determinant of population growth than was fecundity, although the combined effect of all threats on calf mortality was even more influential. Among the threats analyzed and across the ranges for each that we tested, biomass of each of the two prey species had larger effects on population growth than did the rate of PCB accumulation or the impact of noise on prey availability.

With the important caveats that the ranges we have initially tested for each threat might not represent what range is believed to be plausible in future scenarios, and all of the parameter estimates are subject to revision as more data become available, the above results suggest that the population growth is very sensitive to adult survival (as expected for a long-lived, low-fecundity species), and that management that restores prey biomass toward levels closer to the maxima observed in the last few decades could have a significant benefit through much improved calf survival.

DISCUSSION

The project accomplished its primary objective by building a PVA that generates population dynamics that mirrors relatively closely that of the SLE beluga population. Our baseline PVA model that used the average demographic rates observed since 1990 projects growth rates close to zero, in accord with the overall average growth estimated from a Bayesian model fit to data over that time period (Mosnier et al. 2015). However, demographic rates have changed over recent decades, with lower calf survival that is correlated with the increase in sea surface temperature and decrease in ice cover due to climate change and with reductions in prey biomass. The PVA model projects that the population will decline by more than 1% per year under the current environmental conditions. Even in the absence of new threats, amelioration of known existing threats is necessary to return to positive population growth. To reach one stated recovery target of 7,070 individuals by 2100 would require 2.5% annual population growth, but none of the management scenarios examined in the PVA project more than 1% growth.

The PVA revealed that inter-annual variability in calf mortality is the single greatest factor governing the dynamics and recovery of SLE beluga. The range of consequences on population growth caused by threats acting on calf mortality is similar to the range of population trajectories generated by the uncertainty in adult mortality in the model. This is consistent with our understanding of population dynamics of long-lived mammals (Coulson et al. 2000). Sensitivity tests here (Table 5) and elsewhere (e.g., Caswell 2001) indicate that changes in adult mortality could have large impacts on population growth; however, reproduction and infant survival are often influenced much more by environmental factors (Manlik et al. 2016). Pregnancy is less energetically costly in cetaceans than lactation (Williams et al. 2013), so evolution in odontocetes, and probably other marine mammals (e.g., Stenson et al. 2016) may favour a system in which females undertake pregnancy even in years with poor environmental conditions; if the calf does not survive, the mother can try again during her next estrus, when conditions may have improved (Zeveloff and Boyce 1980). Adult mortality is a highly conservative trait in long-lived mammalian species and is expected to be the last trait to be affected by density-dependence or climate variability (Coulson et al. 2000). This sensitivity of population dynamics to changes in calf mortality is likely exaggerated in SLE belugas, because all of the modelled threats act on calf mortality – either correctly or due to data limitations (Figure 16). Previous analyses have found strong relationships between prey variability and calf mortality (Lesage et al. 2014; Plourde et al. 2014), but little evidence was found between changes in prey biomass and pregnancy rate or adult mortality in SLE beluga (Mosnier et al. 2014).

Having built a framework that simulates how big a given population-level effect might be at varying levels of anthropogenic threats, a discussion among scientists and managers is needed to gauge where we consider a population might be along the spectrum for each threat. This may include identifying plausible ranges of threats that might have existed in the past, and may have influenced demographic parameters measured since 1990. It will also apply to threat scenarios that might exist in the future, either under climate change predictions or due to management actions. It is feasible to relate SLE beluga demography to levels of prey abundance for different time periods (Table 3). The PVA can be used to make predictions about demographic consequences of varying levels of contaminants or compromised foraging efficiency, but it is difficult to gauge the most plausible levels to use to describe current threat levels. Rather than considering the PVA outputs as definitive results, it is more useful to consider the product as a quantitative framework for exploring the consequences of different threat levels and to orient future research and management priorities.

The effects of underwater noise and disturbance were modelled as a way of reducing prey available to beluga. By definition, noise could only amplify prey-demography links, so calf mortality was the only vital rate that could be affected by noise in our models. It is currently difficult to assess where the SLE beluga population could fall on the spectrum of compromised foraging efficiency, from negligible to serious. Dedicated field studies, possibly including telemetry, would be needed to quantify any effect of noise and disturbance on foraging efficiency, or to assess whether any other pathway exists to link underwater noise to beluga demography. Once that relationship can be quantified, the PVA can be updated easily to reassess the importance of noise relative to prey abundance, or to estimate the potential conservation gain of reduced levels of noise and disturbance.

Similarly, logistical constraints in laboratory studies restrict inference of the population-level effects of contaminants to an effect of PCB concentration on calf mortality. Contaminants, including PCBs, have been identified as a risk factor for SLE belugas for at least four decades (e.g., Martineau et al. 1987), but predicting the population-level consequences of various PCB concentrations is novel. Given the evidence for declining PCB concentrations (Lebeuf et al. 2014), efforts are needed to predict population consequences of PBDEs and other contaminants, given their high and increasing levels in SLE beluga (Lebeuf et al. 2014). Doing so will be a major undertaking. Methods to predict population-level consequences of PCBs took more than a decade to develop (Hall et al. 2006). One way to proceed might be to undertake an expert elicitation process. Another might be to reexamine the studies included in previous meta-analyses (Hall et al. 2006; Hall et al. 2012; Hall et al. 2011) to assess whether additional information may be available on tissue concentrations of other contaminants. It is likely that some of the underlying studies in previous meta-analyses used lab-grade PCB treatments, whereas others fed laboratory animals fish that happened to contain high levels of PCBs. Some studies may have reported tissue concentrations of PBDEs and other chemicals. Finally, it will be important to continue to monitor for emerging and infectious diseases, to assess whether contaminant-induced immunosuppression could be amplifying the effects of contaminants over and above predicted effects of PCBs on calf mortality.

Across the range of values we considered, uncertainty in current demographic rates and their functional relationships to environmental conditions and threats together contributed twice as much to our uncertainty in the future trajectory of the population as do the ranges of possible management actions that were considered. There is simply no way, using best available data, to quantify effects of noise or contaminants on fecundity or adult mortality. These remain areas for focused study, or for a formal expert elicitation process (Donovan et al. 2016) to assess the extent to which the PVA could be underestimating the population consequences of all stressors on SLE beluga. It would be straightforward to adapt this PVA if new information became available to suggest that adult mortality were affected by stressors in ways that the PVA did not consider. For example, it may be possible to conduct health analyses by sampling pathogens in exhaled breath or measure stress hormones in feces. If a relationship can be derived between stress (i.e., nutritional stress or a stress response to anthropogenic disturbance) and adult mortality, this can be added to the PVA. Similarly, if it were possible to relate nutritional stress or contaminant levels to pregnancy rate, it would be straightforward to add effects of stressors on fecundity in the PVA. For now, this PVA is considered both a living analysis to be updated with new information, and a minimum estimate of the effects of human activities on SLE beluga. If impacts of stressors on additional aspects of demography were documented and added to the models, then projections of various management scenarios may show much more positive results than what we have been able to predict to date. Scenarios considered so far treated environmental factors that have large effects on demography as constants beyond the scope of management, whereas the threats that are more amenable to management were assumed to have comparatively small impacts on demography.

Across the range of stressors we considered, the effects of prey availability contributed most to changes in calf mortality, followed by noise and PCBs (Table 5). All term-wise effect sizes in the PVA are conditional on all other terms being in the model (Table 5). Notwithstanding the known effects of environmental variability on calf mortality, it should be noted that there is substantial additional variance in the data. The PVA prioritizes the relative importance of natural and anthropogenic threats *known or assumed* to be affecting SLE belugas, but the PVA also includes observed variation in demographic rates that cannot be attributed to known causes. This additional variation contributes to uncertainty in predictions of demographic rates from the functional relationships with environmental variables and anthropogenic threats, and indicates that there may be important factors that have not yet been identified (Table 5). Such factors may include harmful algal blooms (HABs, Plourde et al. 2014), but the effects of past HABs are assumed to be subsumed within the "past" and "present" demographic rates used in the PVA (Table 2). If environmental concerns cause the frequency or intensity of HABs to increase, the PVA can be updated easily. Similarly, if new studies reveal an effect of contaminants on adult mortality (e.g., through immunosuppression), additional threat-demography relationships can be added easily. Similarly, the PVA can be updated easily if environmental conditions change in such a way that SLE belugas experience different levels of predation risk or competition with other predators for access to preferred prey species.

In testing the effects of varying levels of threats that might occur or be achieved by management, it is important to keep in mind that the model predictions are conditional on all the other factors in the model. For example, all of the lines predicted for prey and PCB effects would have less negative and possibly some positive slopes if SST and ice conditions are better in the future than what has been observed in the 2008-2012 period that we use to characterize the future regime. It is also possible that demographic rates or other factors in the model are better than has been estimated, so that all projections might be low. The assessments of *relative* impacts of threats and management actions would be more reliable than the predictions of absolute rates of population growth. However, the projections for the various time period regimes (Figure 6) are consistent with observed population dynamics, so the rather pessimistic projections from many of the scenarios presented here might indeed be realistic predictions of future trends.

It is important to examine whether the model predictions make biological sense, validate model predictions as new data on demography and threats become available, and to update the model in an adaptive management framework. If the PVA does make sense to subject-matter and species experts, then a possible next step may be to use the PVA in support of management (e.g., as a Recovery Strategy informs an Action Plan). The PVA revealed that improving prey availability is the factor that would offer the greatest single benefit to the SLE beluga population. Research is needed to gauge whether reducing noise or disturbance could improve foraging efficiency in SLE beluga. If so, mitigating effects of noise may be achievable on a faster timeline than reversing declines in prey stocks, although both tasks are difficult (Williams et al. 2014). Population-level effects of PCBs are expected to be lower than the effects of reduced prey availability, but additional research is needed on effects of PBDEs and other contaminants.

Two main messages emerge from this exercise. First, the population is predicted to do appreciably better if all three main anthropogenic threats could be mitigated in combination (Figure 15) than if mitigation addressed only a single stressor. The population may have been depleted by a single cause (i.e., hunting), but its failure to recover appears to be caused by all three threats, and some mitigation of all three threats may be needed to promote sustained population growth. Secondly, even if all three threats could be mitigated to the most optimistic levels seen since 1990, based on all of the scenarios we tested, none resulted in the population reaching the recovery target of 7,070 individuals by 2100.

ACKNOWLEDGEMENTS

We would like to thank Nicole Bouchard, Christopher W. Clark, Joey Crocker, Jean-François Gosselin, Michael Hammill, Arnaud Mosnier and Yvan Simard for sharing their knowledge and subject matter expertise. We thank all participants at DFO's Marine Mammal Peer Review meeting in Winnipeg in Oct 2016. The authors are responsible for any errors that remain. This study was funded by the Species at Risk programme of Fisheries and Oceans Canada.

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APPENDIX 1: GENERALIZED ADDITIVE MODEL OF EFFECTS OF ENVIRONMENTAL FACTORS AND PREY

MATERIAL AND METHODS

Previous exploratory analyses by Plourde et al. (2014) using a set of 94 variables and principal component analysis (PCA) suggested a negative impact of recent changes in environmental conditions on the St. Lawrence beluga population. In order to further support this observation, Generalized Additive Models (GAMs) were used to explore the potential relationship between the interannual variations in the demography of the beluga population and their habitat quality. Based on Plourde et al. (2014), our general hypothesis was that demographic parameters associated or affecting reproduction success would vary in response to variations in potential prey availability and physical environmental conditions, the likely direct causal mechanisms being through changes in adult female body conditions (unknown parameter). We considered the following demographic parameters derived from Mosnier et al. (2014) model built for the St. Lawrence beluga population: calf mortality, the proportion of pregnant females, adult mortality and the proportion of young individuals. Since PCA could not be integrated into the modelling framework in Vortex, annual values of various physical environment conditions and potential prey were considered in our GAMs in order to describe interannual variations of the summer and winter habitat quality. The predictors included in our analyses were ice duration and volume at the scale of the Gulf of St. Lawrence as a proxy of winter habitat quality, sea surface temperature in summer or in August in the summer habitat and available biomass indices of fish species or groups known to be preyed upon by beluga whales: eel, capelin, mackerel, herring and demersal fishes (Table A.1.1) (Vladykov 1946, Lesage 2014). According to our general hypothesis (Plourde et al. 2014), years characterized by below average ice cover, elevated sea surface temperature and low prey availability would be expected to negatively affect the condition of females (unknown), resulting in demographic characteristics indicative of a lower reproductive success.

The GAMs were fitted with the R package mgcv (v. 1.8-12, Wood 2016) using a Gaussian distribution and an identity link function. Thin plate regression splines were used as smoothers (Wood 2003). The number of predictors (<= 4) and the estimated degrees of freedom for each predictor (k <= 3) were restricted to prevent overfitting and to model biologically realistic functional relationship between predictors and demographic parameters. All combination of four variables or less having a known or assumed effect on the demographic parameters were generated with the dredge function in the R MuMIn package (v.1.15.6, Barton 2016) and compared using the AIC corrected for small sample size (AICc, Hurvich and Tsai 1989). Correlated predictors (Pearson's r > 0.6) were not included simultaneously in models. Interactions between environment and preys were considered but were not selected since the resulting models were overfitted and limited the range of data available for reliable predictions. The best GAMs were selected on the basis on maximizing the % of deviance (%DEV) and the predicting capability (R^2) while minimizing the AICc.

Temporal linear trends of model residuals were verified using the 'gls' function in the 'nlme' package in R (v. 3.1-128, Pinheiro et al. 2016). Temporal autocorrelation in residuals was tested by the 'acf' function in the R 'stats' package (v. 3.3.1 R Core Team, 2016). Conditions of application were verified graphically. The selected GAM for calf mortality respected the conditions of applications and the residuals showed no temporal trends or autocorrelation. The calf mortality GAM was validated using bootstrap. The environmental variables were randomly resampled 1000 times, the GAM refitted and the percentage of deviance calculated. The GAM explained significantly more deviance than random data (P <0.05).

RESULTS

The selected GAMs for the four demographic parameters are presented in table A.1.2. Calf mortality was the sole response variable considered to be associated to interannual variations in habitat quality (physical conditions and prey availability) over the period considered (1990-2012). Variations in calf mortality was best explained by ice cover duration (ICE), sea surface temperature during August (SST), 4T spring herring biomass (HER) and 4Tw demersal species (DEM) which together explained 81.9% of the deviance (Table A.1.2 and Figure A.1.1). The GAM accurately predicted calf mortality (R2=0.73, Fig, A.1.2). HER was kept in the model despite its non-significance because the negative relationship was consistent with the expected effect prey on mortality and because it increased the correlation between observed and predicted data. A GAM considering yellow eel landings instead of HER (both variables were not considered in the same models because they are strongly correlated: r = 0.9) explained a similar %DEV (Table A.1.2). However, the GAM with HER showed a lower AIC and was therefore selected as the best model (-17.8 < -13.5).

Variations in the proportion of pregnant female, adult mortality and the proportion of young individuals were not strongly associated to variations in environmental conditions and prey availability considered in our analyses as illustrated by the quality of the optimal models (Table A.1.2). The predictor's effects were not significant and did not replicate yearly values derived from the population model (Mosnier et al. 2014) as indicated by very low R^2 (<0.3). However, it is noteworthy to mention that the proportion of young individuals in the population was significantly correlated with calf mortality with a lag of 0 (-0.52) and 1 year (-0.55).

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TABLES

Table A1.1. List of variables considered in the GAMs. The GAM column refers to the abbreviation of the variables included in the final selected GAM.

Response Variables

Name	GAM	Description	Period	Source
Calf mortality		Demographic model output	1983-2012	Mosnier et al. 2014
Proportion pregnant		Demographic model output	1983-2012	Mosnier et al. 2014
Adult mortality		Demographic model output	1983-2012	Mosnier et al. 2014
Proportion of young		Demographic model output	1983-2012	Mosnier et al. 2014

Physical

Name	GAM	Description	Period	Source
August SST (SLE)	SST	Mean sea surface temperature in August in the St. Lawrence Estuary	1985-2012	Galbraith et al. 2015
Summer SST (SLE)	SST_{sum}	Mean sea surface temperature from June to August in the St. Lawrence Estuary	1985-2012	Galbraith et al. 2015
GSL Ice cover duration	ICE	Ice cover duration (days) in the Gulf of St.Lawrence	1971-2012	Galbraith et al. 2015
GSL ice cover volume	ICE_{vol}	Mean ice cover volume (km^3) in the Gulf of St.Lawrence	1971-2012	Galbraith et al. 2015

Pelagic fish biomass

Name	GAM	Description	Period	Source
Mackerel 4T		Mackrel spawning stock biomass (tons) determined during the egg survey in southern GSL (4T)	1971-2012	Grégoire et al. 2013a

Name	GAM	Description	Period	Source
Spring herring 4T	HER	Spring herring spawning stock biomass (tons) in 4T	1978-2012	LeBlanc et al. 2012
Fall herring 4T		Fall herring spawning stock biomass (tons) in 4T	1978-2012	LeBlanc et al. 2012
Herring 4T		Sum of spring and fall herring spawning stock biomass (tons) in 4T	1978-2012	
Spring herring 4R		Spring herring spawning stock biomass (tons) in 4R	1971-2015	Grégoire et al. 2013b
Fall herring 4R		Fall herring spawning stock biomass (tons) in 4R	1971-2012	Grégoire et al. 2013b
Herring 4R		Sum of spring and fall herring spawning stock biomass (tons) in 4R	1971-2015	
Capelin 4T		Capelin landings (tons) in 4T	1971-2012	Grégoire et al. 2013c
Capelin 4R		Capelin landings (tons) in 4R	1971-2012	Grégoire et al. 2013c
Capelin 4S		Capelin landings (tons) in 4S	1971-2012	Grégoire et al. 2013c
Eel SLE		Silver American eel counts in Quebec City area estuary traps (Quebec Aquarium)	1971-2012	Cairns et al. 2014
Silver eel SLE		Landings of silver American eels (tons) in the St. Lawrence estuary	1971-2012	Cairns et al. 2014
Yellow eel SLE		Landings of yellow American eels (tons) in the St. Lawrence estuary	1971-2012	Cairns et al. 2014

Demersal fish

Name	GAM	Description	Period	Source
Large species/groups in sGSL (4T)		Biomass (tons) of Cod, Flounder, Haddock, Hake, Redfish, Skates, Marlin-Spike (4T)	1971-2012	Benoît and Swain 2008, Benoît[1] (unpublished data)
Large species/groups in nGSL (4T, 4S,		Biomass (tons) of Cod, Flounder, Haddock, Hake, Redfish, Skates, Marlin-Spike in the nGSL	1990-2012	Bourdages and Ouellet 2011

Name	GAM	Description	Period	Source
4R)				
Small species/groups in nGSL (4T, 4S, 4R)		Biomass (tons) of Lampreys, Lycodes, Lumpfish, Rockling, Sculpins-Cottidae, Snailfish in the nGSL	1990-2012	Bourdages and Ouellet 2011
Large species/groups (4Tw)		Biomass (tons) of Cod, Flounder, Haddock, Hake, Redfish, Skates, Marlin-Spike (4Tw)	1990-2012[2]	Bourdages and Ouellet 2011
Small species/groups (4Tw)		Biomass (tons) of Lampreys, Lycodes, Lumpfish, Rockling, Sculpins-Cottidae, Snailfish in the (4Tw)	1990-2012[2]	Bourdages and Ouellet 2011
Dermal species (4Tw)	DEM	Sum of biomass of small and large dermersal species (4Tw)	1990-2012[2]	
Preys in the summer habitat (SLE)		Biomass (tons) of spring herring (4T), large species/groups (4Tw), small species/groups(4Tw), yellow eel landings (SLE)	1990-2012[2]	
Preys in the winter habitat (GSL)		Biomass (tons) of spring herring (4R), fall herring (4R), large species/groups (4T), small species/groups(nGSL), Capelin (4R, 4S)	1990-2012	

[1] Fisheries and Oceans Canada, Moncton, NB Canada

[2] *1993 and 2003 removed from analyses because of abnormal capturability*

Table A1.2. Results of selected GAMs describing the relationship between demographic parameters and the environment. The AIC is corrected for small sample size (AICc).

Response variables	Variables selected	%DEV	R^2	AICc
Calf mortality	ICE** + SST** + HER^{ns} + DEM*	81.9	0.73	-17.8
	ICE* + SST** + EEL^{ns} + DEM*	81.5	0.71	-13.5
Proportion pregnant	ICE^{ns} + HER^{ns} + DEM^{ns}	20.9	0.05	-20.0
Adult mortality	ICE^{ns} + SST^{ns} + HER^{ns} + DEM^{ns}	39.3	0.14	-118.6
Proportion young[1]	ICE^{ns} + SST^{ns} + HER^{ns} + DEM^{ns}	41.1	0.26	-88.1

p-value of smooth terms and correlation coefficients are indicated by : ns > 0.05; * 0.05 - 0.01; ** 0.01 - 0.001

[1] Proportion young at year *y* is correlated to calf mortality at year *y* (-0.52) and *y*-1 (-0.55).

FIGURES

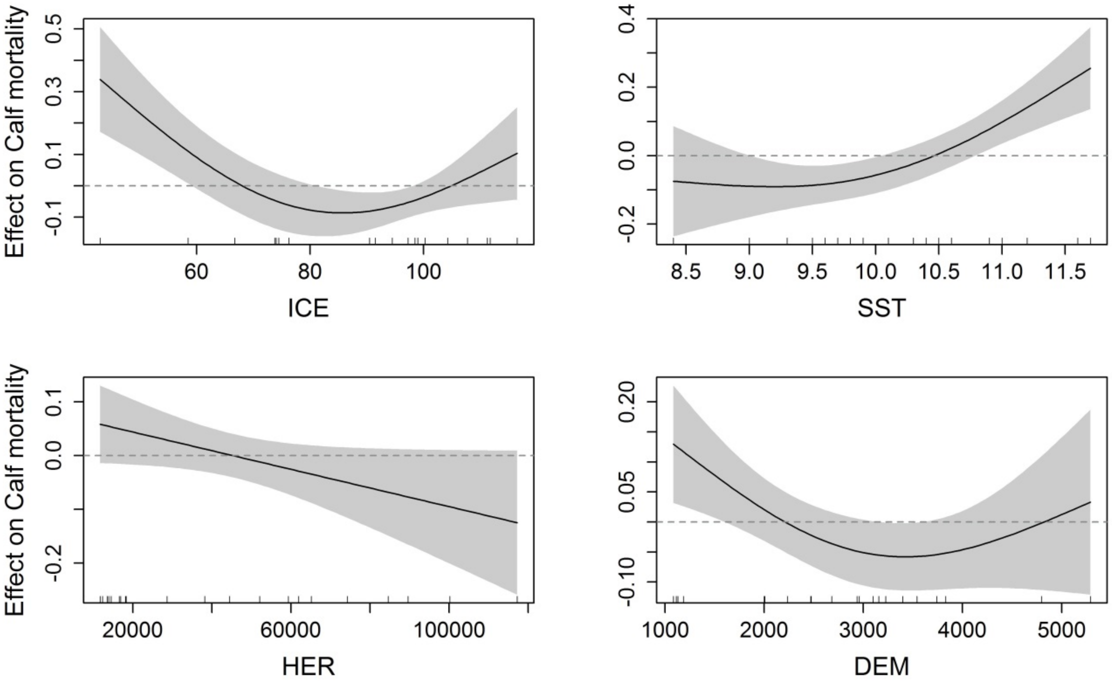

Figure A1.1. Results of the selected GAM showing the effect of the environment and preys on calf mortality. Tick marks on the x-axis represent the location of data points. The 0 value on the y-axis and the dashed line represent the mean mortality (0.287). The solid line represent the main effect which is either positive above the dashed line (increase in mortality) or negative below the dashed line (decrease in mortality). The shaded area represents 95% confidence intervals.

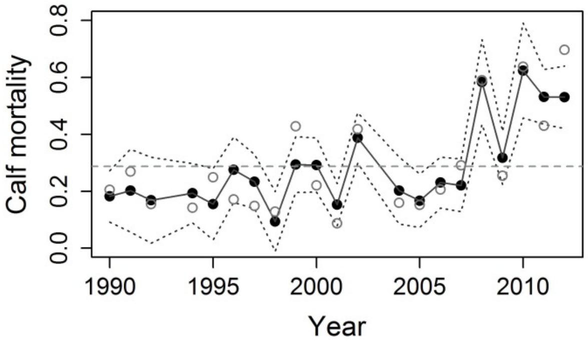

Figure A1.2. Performance of the selected GAM. Open circles indicate observations. Black circles rand the dotted black lines represent the mortality predicted by the selected GAM and the uncertainty (±2 SD) around the predicted values respectively. The grey dashed line represents the mean calf mortality.