

# Climate change complicates efforts to ensure survival and recovery of St. Lawrence Estuary beluga

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## ABSTRACT

Decades after a ban on hunting, and despite focused management interventions, the endangered St. Lawrence Estuary (SLE) beluga (*Delphinapterus leucas*) population has failed to recover. We applied a population viability analysis to simulate the responses of the SLE beluga population across a wide range of variability and uncertainty under current and projected changes in environmental and climate-mediated conditions. Three proximate threats to recovery were explored: ocean noise; contaminants; and prey limitation. Even the most optimistic scenarios failed to achieve the reliable positive population growth needed to meet current recovery targets. Here we show that predicted effects of climate change may be a more significant driver of SLE beluga population dynamics than the proximate threats we considered. Aggressive mitigation of all three proximate threats will be needed to build the population's resilience and allow the population to persist long enough for global actions to mitigate climate change to take effect.

## 1. Introduction

The southernmost of the beluga populations, the St. Lawrence Estuary ("SLE") beluga (*Delphinapterus leucas*), is geographically and genetically isolated from 28 other populations of beluga distributed throughout the circumpolar region of the Arctic (Committee On the Status of Endangered Wildlife in Canada, 2014). Before hunting practices ended in 1979, overharvest depleted the SLE beluga population by ~87–90% of its size at the turn of the 20th century to ~1000 individuals (Fisheries and Oceans Canada, 2014a, 2014b). Unlike baleen whale and pinniped populations that rebounded following the cessation of hunting (Clapham et al., 1999; Schipper et al., 2008; Thomas et al., 2016), several depleted populations of highly social odontocetes have failed to show the expected recovery (Wade et al., 2012). The SLE beluga population did not show statistically significant signs of increase between 1988 and 2005, despite intensive monitoring and implementation of multiple management measures for mitigating lethal and sublethal anthropogenic threats (Hammill et al., 2007). The cause(s) for the failure to recover are unclear, but likely stem from the cumulative effects of

multiple stressors, rather than a single driver (Fisheries and Oceans Canada, 2014a, 2014b). Lethal threats, including ship strikes and entanglement in fishing gear, are rare (Lair et al., 2016). Sublethal threats to recovery included: ocean noise, toxic contaminants, and prey limitation (Lesage, 2021). Stochastic, catastrophic events, such as harmful algal blooms (HABs) or oil spills, increase extinction risk but pose a particular challenge to predict, prevent, or mitigate.

Beluga in the SLE live downstream of a highly industrialized and urbanized region discharging large volumes of toxic substances into the St. Lawrence River (e.g., Martel et al., 1986; Lebeuf and Nunes, 2005). Decades of exposure has led to high levels of a variety of pollutants in beluga tissue including mercury, DDT, PCBs, Mirex, toxaphene, PAH, dioxins and furans (reviewed by Lebeuf, 2009; see also Lebeuf et al., 2014a; Simond et al., 2017; Martineau et al., 1987). While several of these substances have decreased in the beluga environment since at least 1987, others such as toxic flame retardants (PBDEs) have increased exponentially in the 1990s, and remain at maximum levels in beluga tissues since then (De Wit, 2002; Lebeuf et al., 2014b; Lebeuf et al., 2014a; Simond et al., 2017). These toxic substances and other persistent

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organochlorine pollutants can disrupt endocrine functions, with possible impacts on reproduction, immunity, behaviour and offspring development (reviewed in Lebeuf, 2009; Lebeuf et al., 2014a; see also Costa et al., 2014; Yu et al., 2015). PBDE homologs can negatively affect blood thyroid hormone levels in beluga (Villanger et al., 2011). In SLE beluga, a correlation has been documented between thyroid-related gene expression and levels of some emerging halogenated flame retardants (Simond et al., 2019). The strikingly high incidence of cancers in SLE beluga compared to other wild mammal populations has been attributed to high PAH exposure prior to the 1980s (Martineau et al., 2002). Cessation of PAH emissions and banning of PCBs in the 1970s are thought to be responsible for the progressive disappearance of some neoplastic diseases recently documented in SLE beluga (Martineau et al., 2002; Lair et al., 2016; Poirier et al., 2019).

Chronic elevation of ambient noise levels and repeated disruption of normal activity as a result of thousands of ship transits into SLE beluga habitat, a multi-million dollar whale-watching industry, multiple ferry operations, and recreational activities is also viewed as a potential threat to SLE beluga (Blane and Jaakson, 1994; Simard et al., 2010; McQuinn et al., 2011; Gervaise et al., 2012; Ménard et al., 2014). Vessel traffic and beluga-oriented nautical activities (even if prohibited in some sectors) peak in July–August, when SLE beluga give birth (Sergeant, 1986). Vessel noise and presence has been shown to cause masking of contact calls and reduce communication space in SLE beluga, to alter the characteristics of their calls or result in termination of communication or change in behaviour (Blane and Jaakson, 1994; Lesage et al., 1999; Scheifele et al., 2005; Gervaise et al., 2012; Vergara et al., 2021).

A population model incorporating multiple sources of demographic data 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). The long-term objective of one recent Recovery Strategy was to return the population to approximately 7000 individuals, or 70% of its historical size, by 2100 (Fisheries and Oceans Canada, 2014a, 2014b). An intermediate objective of 1000 mature individuals was specified to reduce the probability of extinction risk in the shorter term (Fisheries and Oceans Canada, 2014a, 2014b). Although the underlying cause of the decline was clear—historical overharvesting—the recovery strategy recognized that promoting population growth would require assessing the cumulative impacts of multiple lethal and sublethal stressors. When a population faces multiple stressors, it is important to compile quantitative information on population responses to changing environmental conditions to inform management and guide evidence-based decisions (Williams et al., 2016; Lacy et al., 2017; Ashe et al., 2021). The aim of this paper is to construct a population viability analysis (PVA) model to estimate population-level effects from both natural and anthropogenic threats, as well as possible management actions. Population trajectories predicted through these models will provide insight into key management areas and effective mitigation strategies for the recovery and growth of SLE belugas, and allow managers to set recovery targets that are biologically achievable.

## 2. Methods

A population viability model (PVA) was constructed in Vortex 10 (Lacy et al., 2014; software and manual available at [www.scti.tools](http://www.scti.tools)) to simulate the effects of both intrinsic demographic rates and environmental and anthropogenic stressors on the SLE beluga population. As implemented in Vortex, the PVA is an individual-based simulation model (Ashe et al., 2021).

We constructed the PVA to estimate the population-level effect of an externally imposed stressor on SLE belugas and compared demographic measures in the presence or absence of the stressor. The analytical approach to integrating natural demographic processes and anthropogenic threats, including uncertainty, is described below. The three proximate threats considered are the anthropogenic threats identified in

the recovery strategy (DFO, 2012), and the latest status review (Fisheries and Oceans Canada, 2014b), namely (a) prey limitation (“prey”); (b) PCBs and other contaminants (“contaminants”); and (c) reduced prey acquisition via disturbance and acoustic masking from underwater noise from vessels (“noise”).

Prey was incorporated as a functional relationship between spring herring and demersal prey biomass and calf mortality (while also including the effects of sea surface temperature and ice cover), based on empirical diet studies (Lesage et al., 2020). 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).

Contaminants were included while accounting for maternal PCB load and its effect on the probability of survival of each calf. The proportion of maternal PCBs accumulated by the fetus during gestation was set at 0.6, and a further 0.77× of the maternal PCB level is transferred during lactation (as estimated from published data for other cetacean species; see Hall et al., 2018 for details). 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.

To explore the effects of changing noise levels, we tested scenarios where the prey biomass is multiplied by factors of 0.75×, 0.90×, 1.0× (management baseline), 1.1×, and 1.25× to represent accessible prey abundance. The choice of a 25% reduction in foraging efficiency, due to some combination of acoustic masking and behavioural 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). Studies on narwhal and beluga in the Canadian Arctic have found both species to be extremely sensitive to ice-breaker noise, and are responding to sounds at the edge of audibility (Cosens and Dueck, 1993). Assuming that SLE beluga are about as sensitive to vessel-based disruption of feeding as the urban southern resident killer whale seems like a reasonable placeholder, until new information becomes available. 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 (e.g., Gervaise et al., 2012; Williams et al., 2019). 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.

In addition, changing climatic conditions was identified as a potential factor in the decline or in hindering recovery of the beluga population (DFO 2014). 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). We used generalized additive models to understand how decadal-scale changes in SST and ice cover influenced SLE beluga carcass detections, and included these model outputs in our PVA. Additional technical details on the PVA modelling methods and results are provided in the Supplementary Materials and in Williams et al. (2017).

In the initial PVA, we simulated one population over 100 years for 10,000 iterations (see input parameters in Table 1). Extinction was defined as no males or females remaining. No adjustment was made for inbreeding depression, because initial population size was large enough to make significant inbreeding unlikely for a long-lived species. The mating system was assumed to be polygynous, with new selections of

**Table 1**

Beluga population parameter model inputs. SLE beluga population parameters used as inputs to program Vortex for the initial population viability analysis model.

Parameter	Value
Female age at first reproduction	Range: 8–14 <sup>a,b,c</sup>
Male age at first reproduction	Range: 12–22 <sup>a,b,c,d</sup>
Female age of senescence	Range: 45–75 <sup>e</sup>
Sex ratio at birth	50:50
Males in breeding pool	Assumed to be polygynous
Maximum number of litters per year	1 <sup>f</sup>
Maximum number of progeny per litter	1 <sup>f</sup>
% adult females that breed each year	0.326 (CI 95% = 0.276–0.369) <sup>g</sup>
Environmental Variation (EV) in breeding	Range: 0–0.12
Adult mortality rate	Median: 0.061 (CI95%: 0.050–0.072) <sup>g</sup>
Calf mortality rate	Median: 23.7% (CI95%: 0.165–0.327) <sup>g</sup>
Environmental Variation (EV) in calf mortality	Range: 0–0.12 <sup>h</sup>
Initial population size	900
Carrying capacity	8000 <sup>i</sup>

<sup>a</sup> Brodie, 1971.

<sup>b</sup> Sergeant, 1973.

<sup>c</sup> Heide-Jørgensen and Teilmann, 1994.

<sup>d</sup> Finley, 1982.

<sup>e</sup> Burns and Seaman, 1986.

<sup>f</sup> Lesage and Kingsley, 1998

<sup>g</sup> Mosnier et al., 2015 (See also: Kleinenberg et al., 1964; Sergeant and Brodie, 1975; Burns and Seaman, 1985; Doidge, 1990).

<sup>h</sup> Mosnier et al., 2014.

<sup>i</sup> DFO Recovery Strategy (DFO, 2012).

mates each year. Sex ratio (percent males) at birth was assumed to be 50%. Carrying capacity was set to 8000 (i.e., somewhere between the DFO recovery target of 7070 and the 8000 to 10,000 estimated to have been in the population in the late 1800s). It is important to note here that the PVA was insensitive to this somewhat arbitrary choice, because the population trajectory never reached 8000.

Maximum lifespan was set to 75 years, and the reproductive senescence of females was set to a mean of 50 years. Females were assumed to be sexually mature as early as age 8, with individual females modeled as being sexually mature beginning at age 8 to 12 (therefore usually producing their first calf by 14 y, based on the breeding rate of mature females, below, of 32.6% per year). Females are assumed to cease breeding between age 45 and 55 and males are assumed to breed from age 12 to the maximum age. Individual males are capable of starting breeding at age 12 to 14.

Mortality rates (means with 95% confidence intervals) were obtained from Mosnier et al. (2015). Given that the confidence interval is approximately  $\pm 2$  SD, we estimated the uncertainties in each parameter with an SD set to  $\frac{1}{4}$  of the span of the 95% confidence interval. Maximum levels of annual variability 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). Lacy et al. (2014) describes the methods to remove sampling error from estimates of annual variation in fecundity and calf survival (EVs). The rationale for the choice of these and all other demographic parameters is given in Table 1, unless otherwise specified.

### 2.1. Initial population model

An initial population model was applied 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 a normal distribution with the mean

parameter estimate and standard deviation estimated from the reported confidence interval. 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 modeled as separate causal factors determining the demographic rates.

### 2.2. 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 to 1999, a period that can be described as the “Past” regime, SST was lower, ice duration longer, and prey availability (i.e., demersal prey and herring biomass) was 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 demersal prey and herring biomass much lower than previously (see also Plourde et al., 2014). These trends, particularly those in physical conditions, continued in the most recent years, and the period 2008–2012 might best represent the regime under current climate change scenarios (Loder et al., 2015). We therefore examined three climate change regimes (each using the 2000–2012 levels of prey): “Climate-SST” projects future SST to be as observed 2008–2012; “Climate-ICE” projects future ice to be as observed 2008–2012; “Climate-SST + ICE” projects both environmental conditions to remain at 2008–2012 levels. Thus, for each scenario, we tested climate conditions as observed in one of the time periods, but we did not attempt to predict future conditions that might arise if the climate continued to change.

### 2.3. 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 (Louder 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 Herring, Demersal 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 factor (Herring, Demersal, Noise impacts on prey accessibility, and PCB accumulation rate) across several levels spanning a wide range of values. For Demersal and Herring 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 0.75 $\times$  to 1.25 $\times$ . For PCB models, we tested rates of accumulation that varied from 0 to 4 mg / kg lipid / y. In four “Multi-threat models” we tested some combinations of two or more of the threats being reduced simultaneously to the best conditions tested in the single-threat models. Single-threat management scenarios are included in the Supplementary Materials.

Finally, we ran a scenario 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

**Table 2**

Environmental and prey variables. Means and SDs of the environmental and prey variables during each regime applied to the SLE beluga PVA. 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	80,187 (0.684)	19,997 (0.180)	2796 (0.529)	1469 (0.278)
Present:2000–2012	10.52	0.74	81.52	19.16	20,944 (0.179)	9921 (0.088)	2766 (0.523)	914 (0.173)
Climate-SST: 2008–2012	11.10	0.64	81.52	19.16				
	(2008–2012)							
Climate-ICE	10.52	0.74	73.40	25.21				
			(2008–2012)					
Climate-SST + ICE	11.10	0.64	73.40	25.21				
	(2008–2012)		(2008–2012)					

**Table 3**

Management scenarios. 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.

Scenario	Herring (mean relative index)	Demersal (mean relative index)	Noise (impact on prey accessibility)	PCB (accumulation rate; mg/kg/y)
Management baseline (2000–2012)	0.179	0.523	1×	2
Prey management				
Prey-HER (1990–1999)	0.684	0.523	1×	2
Prey-DEM (2000–2012)	0.179	0.529	1×	2
Prey-DEM + HER (1990–1999)	0.684	0.529	1×	2
Multi-threat models				
Reduced Noise + no PCBs	0.179	0.523	1.25x	0
Maximum Prey	1.0	1.0	1×	2
Max. Prey + no PCBs	1.0	1.0	1×	0
Max. Prey + no PCBs + reduced Noise	1.0	1.0	1.25x	0

that we examined.

The impacts of varying levels of Herring, Demersal, Noise, and PCBs (Supplementary Materials) 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 (i.e., to span the range from increased impacts of noise on foraging to approaches to mitigate impacts of ship and boat noise on SLE beluga, (e.g., Williams et al., 2019), and the rate of PCB accumulation was sampled from a uniform distribution from 0 to 4 ppm / year (i.e., to span the range from complete elimination to worsening). 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.

The Vortex input file (SLEBeluga.xml) used in the Vortex modelling is available in the [zenodo.org](https://zenodo.org) repository at <https://doi.org/10.5281/zenodo.4541787>.

### 3. Results

#### 3.1. Initial population model

The mean population growth rate projected from the long-term

average demographic rates was marginally positive, with  $r = 0.0002$ . Fig. S1 shows the mean trajectory ( $\pm 1$  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. 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. The uncertainty in trajectories over time and among iterations is shown in Fig. S2 with 100 sample iterations of this initial model.

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 shown in Table 4. Uncertainty in 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. 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.

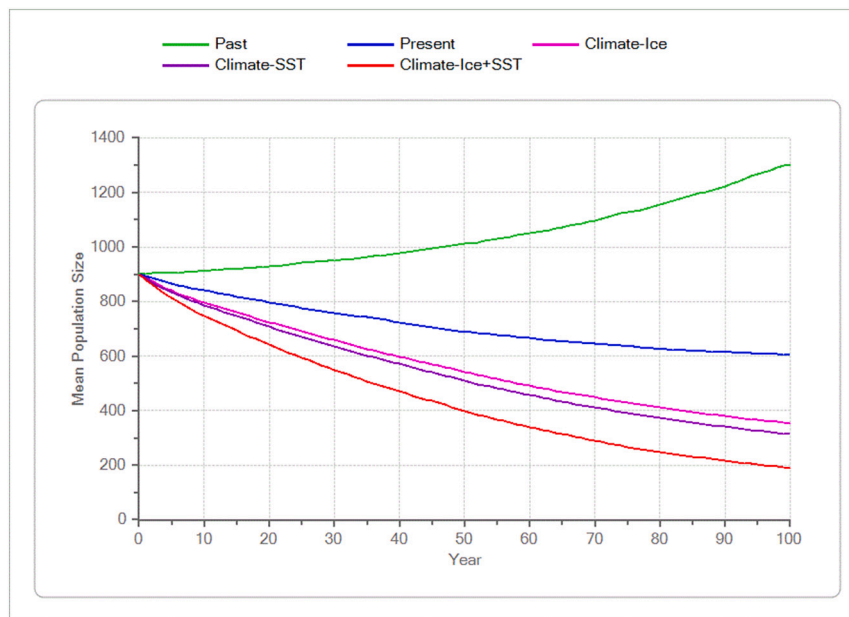
#### 3.2. Time period regimes

Fig. 1 compares the mean trajectories projected under regimes representing the environmental and prey conditions during different time periods. Under the “Past” conditions from 1990 to 1999, mean population growth is expected to be marginally positive ( $r = 0.001$ ), but with large uncertainty that includes the possibility of population decline ( $SD(r) = 0.022$ ). Under the “Present” conditions (since 2000), mean population growth is projected to be slightly negative, but with a range of projections that includes the possibility of growth ( $r = -0.007$ ,  $SD =$

**Table 4**

Variance in population growth rate. 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



**Fig. 1.** Mean Projected Population Sizes Under Various Regimes. 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).

0.026). If ice duration is projected to be lower, as it was 2008–2012, then population decline is projected to be faster ( $r = -0.012$ ,  $SD = 0.030$ ). And, 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. A population decline is projected ( $r = -0.019$ ,  $SD = 0.032$ ) for the scenario that tests various management options (“Climate-Ice+SST”). This scenario includes recent (2008–2012) sea temperature and ice conditions, but with prey biomasses typical of the 2000–2012 period.

### 3.3. Prey management scenarios

The mean population trajectories predicted from scenarios that test improvements in Herring, Demersal, or biomass of both prey species to the levels observed in 1990–1999 are shown in Figs. S6 and S7. This change to Demersal biomass has almost no effect on the population projections, because the mean Demersal biomass was roughly equivalent in the periods 1990–1999 and 2000–2012 (Table 2). However, within each of these time periods, there were large fluctuations in Demersal biomass, shown by the large associated standard deviations. Given the significant influence of Demersal biomass on calf mortality, improvements to Demersal biomass have the potential to confer beneficial effects on the SLE beluga population growth rate (e.g., Fig. S7). When the Demersal prey was set to the 1990–1999 levels, SLE population growth decreased slightly relative to the Management Baseline (Fig. S7). Again, due to the strong link between Demersal biomass and calf mortality, the larger annual demersal variation in the earlier decade leads to more years in which a lack of Demersal prey reduces calf survival. Herring biomass was almost 4-fold higher in 1990–1999 than subsequently (Table 2). If Herring are returned to the higher levels reported in the 1990s, the population growth rate is projected to rise to  $r = -0.013$  from the  $r = -0.019$  in the Management Baseline (Fig. S6).

### 3.4. Multi-threat management scenarios

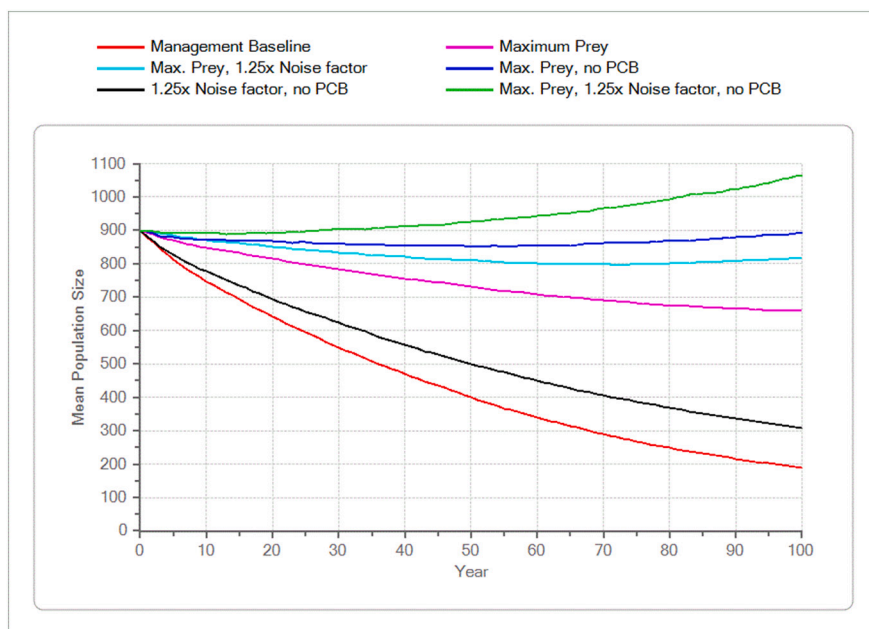
The analyses presented in the supplementary materials indicate that amelioration of any one of the three proximate threats alone, within ranges that seem feasible to change from management intervention, are

not sufficient to achieve sustained positive population growth. The management actions are not sufficient to overcome the predicted negative impacts of warming sea temperatures and decreased ice. Therefore, we tested scenarios in which improvements were made to the several threats in combination (Fig. 2).

Intervention actions toward restoring prey biomass, increasing feeding efficiency via reduction in noise disturbance, and removing PCBs from the environment would be required to achieve consistent positive population growth in the model (Fig. 2). Even under this most optimistic scenario, the population is projected to grow only 0.3% per year. The higher SST and low ice duration are predicted to continue to depress calf survival, thereby slowing projected population growth for the population as a whole. However, an increase in prey biomass coupled with removal of PCBs (“Max. prey, no PCB”) would also allow an eventual return to positive population growth, but not until the PCB loads in the current population are eliminated through depuration and population turnover.

### 3.5. Comparing threats in a comprehensive model

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% (Table 5). The uncertainty in functional relationships of the variables included in the GAM as well as the PCBs to calf mortality, account for most of the remaining 26% of the variation. Inherent demographic stochasticity contributes a small amount to the residual variation in projected population growth in the model. 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. Yet, the combined effect of all threats on calf mortality was even more influential (Table 5). Among the threats analyzed and across the ranges for each that we tested, biomass of each of the two prey groups had larger effects on population growth than did the rate of PCB accumulation or the impact of noise on prey accessibility.



**Fig. 2.** Mean population sizes projected if the current environmental conditions (period 2008–2012) and recent prey biomasses (2000–2012) persist (“Management baseline”), both Herring and Demersal prey 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 1.25× (“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”).

**Table 5**

Proportion of variance in the population growth rate with threats. 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, Herring, Demersal, Noise, and PCB) to calf mortality, as well as the inherent unpredictability of population demographic processes.

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

**4. Conclusions**

The SLE beluga population is unlikely to recover to pre-exploitation levels or meet interim recovery targets, even under our most optimistic scenarios, because the reproductive capacity has been reduced both by sublethal threats and by climate changes observed in the decades since cessation of harvest (Fig. 1). To achieve consistent positive population growth, actions that support an increase in calf survival, restoring prey biomass, increasing feeding efficiency via reduction in noise disturbance, and removing PCBs from the environment would all be required to buffer the population's resilience to future projections of climate change (Fig. 2). Even under this most optimistic scenario, the population is projected to grow only 0.3% per year due to the predicted higher SST and low ice duration that continue to depress calf survival. The increase in prey biomass coupled with removal of PCBs alone, however, is another pathway toward an eventual return to positive population growth, but first, PCB loads in the current population would need to be eliminated through depuration and population turn-over.

Climate change did not cause the population's threatened status and is not alone responsible for the population's negative growth, but has made the task of recovery more difficult as it might have reduced the population resilience to buffer other stressors. Our work shows that climate change impacts, along with other large-scale, long-term, pervasive aspects of environmental degradation, are reducing the capacity or biological scope for species to absorb and rebound from short- or longer-term stressors (human depletion of food supply, pollution that stresses physiological systems, periodic disturbance, disease outbreaks, etc.). For instance, climate change might exacerbate negative effects of vessel traffic on feeding efficiency or opportunities by reducing key prey abundance and distribution. This pattern is consistent with similar population recovery failures seen in other highly social odontocetes, including sperm whales, narwhal, eastern tropical Pacific dolphins, southern resident killer whales, and pilot whales (Wade et al., 2012). The mechanism for this is unclear. Harvests that result in relatively large depletions in the size of social odontocete populations appear to reduce the capacity of that population to recover (Wade et al., 2012). In contrast, many baleen whale populations have recovered to pre-whaling numbers after cessation of whaling (Bejder et al., 2016; Moore et al., 2001; Zerbini et al., 2019). However, there is evidence to suggest that highly social odontocetes, including killer whales and bottlenose dolphins, can adjust their foraging behaviour in response to long-term changes in climate conditions and prey density (Lusseau et al., 2004).

**4.1. Model limitations**

As with any model of complex natural systems, the simplifications in the model structure and data input limit the precision and accuracy of projections of future population dynamics. First, the model projections can only be as accurate as the parameter estimates that are used. We addressed this limitation by including uncertainty in model inputs in the model structure. Moreover, the Vortex population model includes more sources of stochasticity in population processes – such as annual variation in demographic rates, demographic stochasticity, variable sex ratio, individual variation in age of maturity and senescence – than are included in most wildlife population models. We did not include density dependent effects, such as an Allee effect whereby reproduction might be reduced when the population becomes small and individuals widely dispersed, nor did we include inbreeding depression that could depress

survival and fecundity after the population declines to very small size. Thus, it is possible that our projections underestimate the risk of collapse and extinction if the population declines substantially further.

Most importantly, PVA models can reveal the likely effects only of those threats about which we have knowledge and can incorporate into the model via plausible parameter estimates. Other threats – such as oil spills, other contaminants, or harmful algal blooms – might contribute to past and future declines. To the extent that such factors influenced observed past demographic rates, they would be included in the population model as a component of mean rates and annual variation in rates. However, our model does not inform us about the possible impacts if as yet unexamined threats either increase or decrease from current levels. With respect to threats that we modeled, both the model of PCB accumulation and impacts and the model of reduction in feeding caused by noise disturbance were based on studies on other cetaceans. Further research would be needed to determine how accurately these relationships apply to the SLE beluga. The GAM analyses used to characterize the impacts of climatic variables and prey abundance on beluga demography are correlational and might not reflect direct causal relationships. Thus, the variables should be viewed as indicators of environmental changes, not necessarily as the direct factors to which the beluga population is responding. Our population model included some interactions among threats, such as the effect of noise on time spent feeding and interacting with prey abundance to determine accessibility of prey to the beluga, but other interactions that were not yet explored might also be important.

As we move from exploring hypothesis to obtaining empirical parameter estimates on threats, an important next step will be to integrate these into a Population Consequences of Multiple Stressors (PCoMS) model to explore potential antagonistic, additive, or synergistic effects (National Academies of Sciences, 2017). For example, as prey biomass improves, there is potential that the negative effects of PCBs on population growth rate may be reduced by a variety of biological pathways. Lipophilic PCBs have been shown to mobilize more readily in prey-limited, nutritionally-compromised cetaceans than in animals that are not nutritionally stressed (Kannan et al., 2000; Houde et al., 2005; Jepson et al., 2016). If ocean noise levels decrease, this may improve foraging efficiency (Lesage et al., 1999; Lusseau et al., 2009; Williams et al., 2006; Williams et al., 2021), potentially buffering impacts of PCBs on calf survival and immunosuppression (Hall et al., 2018).

Under the US Marine Mammal Protection Act, the United States sets allowable harm limits for incidental human-caused mortality (e.g., due to fisheries interactions) of whales, dolphins and porpoises based on a default annual population growth rate of 4% (Wade, 1998). These allowable harm limits assume that populations can withstand a “take” of perhaps half of this potential for excess growth, with precautionary reductions for endangered or poorly studied species. Climate change, combined with the cumulative impact of multiple anthropogenic stressors, has resulted in some populations having growth rates well below the default value of 4%, so that recovery after anthropogenic or even natural perturbations is no longer possible under time frames that may once have been biologically plausible. Lower, and therefore more precautionary, harm limits may need to be considered for populations whose resilience is compromised by degraded habitat or cumulative effects of sublethal stressors (Williams et al., 2016).

#### 4.2. Recommended management strategies

Our findings suggest that SLE beluga population growth is very sensitive to changes in adult survival (as expected for a long-lived, low-fecundity species), and that management measures that support prey biomass recovery near levels observed in the last few decades could have a significant benefit through much improved calf survival. An important caveat, however, is 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 or functional relationships to environmental conditions and threats are subject to revision as more data become available. Adult mortality is a highly conserved 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 modeled threats act on calf mortality – either correctly, or due to data limitations. Previous analyses have found strong relationships between prey variability and calf mortality (Lesage et al., 2014; Plourde et al., 2014), but little evidence for a link with pregnancy rate or adult mortality has been found in SLE beluga (Mosnier et al., 2014). The SLE beluga population represents a polar species at the southernmost limit of its distribution, now restricted to a boreal, warming habitat (Fisheries and Oceans Canada, 2014a, 2014b). Our analyses show that the status quo will most probably lead to continued decline in this relict population. The population viability analyses revealed that only the most aggressive threat mitigation scenarios (i.e., continued reductions in PCB levels; reduction of ocean noise and disturbance; alterations to fishing quotas to increase prey availability) resulted in sustained population growth. These proximate anthropogenic threats have removed the potential for robust growth, and climate change now exacerbates the threats and pushes a previously stable or slightly growing population into a decline. Of these proximate threats, effective mitigation for low prey abundance through fisheries management actions would offer the greatest single benefit to the SLE beluga population (Supplementary Material), but it is arguably the most limited. There is currently little fishing on any of the major beluga prey species, or on beluga competitors for these prey in the SLE or northern Gulf of St. Lawrence (spring herring, capelin, sandlance, cod). Of these species, only the low cod population size is arguably due to overfishing, and currently, this fishery is all but closed. Research is needed to gauge whether reducing noise or disturbance could improve foraging efficiency in SLE beluga (e.g., by slowing ships (Williams et al., 2021)). If so, mitigating effects of noise may be achievable on a faster timeline than reversing declines in prey stocks (Williams et al., 2014, 2019). Mitigating the proximate threats is more tractable than reversing global climate change, and can result in population persistence – and even slow recovery – if the climate does not continue to deteriorate for the SLE beluga. Absent a commitment to reverse the long-term effects of climate change, realistic expectations for this Endangered population must be reduced to persistence, rather than recovery to former levels.

#### CRedit authorship contribution statement

**Rob Williams:** Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition. **Robert C. Lacy:** Conceptualization, Methodology, Software, Validation, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Erin Ashe:** Conceptualization, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration, Funding acquisition. **Ailsa Hall:** Methodology, Formal analysis, Writing – original draft, Visualization. **Stéphane Plourde:** Methodology, Software, Writing – original draft, Writing – review & editing, Visualization. **Ian H. McQuinn:** Methodology, Writing – original draft, Writing – review & editing. **Véronique Lesage:** Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing, Supervision.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

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