



Incorporating environmental covariates into a Bayesian stock production model for the endangered Cumberland Sound beluga population

Brooke A. Biddlecombe^{1,2,*}, Cortney A. Watt^{1,2}

¹Freshwater Institute, Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada

²Department of Biological Sciences University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada

ABSTRACT: The Cumberland Sound (CS) beluga (*Delphinapterus leucas*) population inhabits CS on eastern Baffin Island, Nunavut, Canada, and is listed as threatened under the Canadian Species at Risk Act. The population dynamics of CS beluga whales have been modelled in the past, but the effect of environmental covariates on these models has not previously been considered. An existing Bayesian population model fitted to CS beluga whale aerial survey data from 1990 to 2017 and harvest data from 1960 to 2017 was modified to include sea ice concentration (ICE) and sea surface temperature (SST). ICE and SST were extracted for all years from the CS study area in March and August, respectively, and incorporated into the state process component of the state-space model. The model resulted in a 2018 population estimate of 1245 (95 % credible interval [CI] 564–2715) whales and an initial population estimate of 5147 (95 % CI 1667–8779). Determining sustainable harvest by calculating the probability of population decline estimated 30 % probability of decline after 10 yr with a harvest of ~15 whales annually. Compared to the previous model without environmental covariates, which followed a relatively linear trajectory, our model had more noticeable peaks and troughs in the population trend and wider CIs. The model suggested harvest levels be reduced by ~7 individuals for a management goal with a low risk of decline. The novelty of this approach for beluga whales provides an opportunity for further model development via the addition of various other abiotic and biotic variables related to beluga whale ecology.

KEY WORDS: Beluga · Population dynamics · Sea ice · Sea surface temperature · Bayesian model · Harvest

1. INTRODUCTION

Beluga whales *Delphinapterus leucas* are toothed whales with an extensive history of subsistence use by Inuit in the Arctic which continues today (Richard & Pike 1993, Wenzel 2009). Cumberland Sound (CS) beluga whales are a separate beluga stock that spends summers in northern CS, commonly aggregating in Clearwater Fiord (66.6° N, 67.4° W), and the rest of the year in the main waters of CS (de March et al. 2002, 2004, Richard & Stewart 2008, Turgeon et al. 2012) (Fig. 1). The CS beluga population was sig-

nificantly reduced by commercial whaling between 1868 and 1939 (Mitchell & Reeves 1981). CS belugas are the only beluga population listed as threatened under the Canadian Species at Risk Act (SARA 2017) and are considered endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2004). This listing makes this a population of interest, as harvest levels can have potentially severe impacts on the population trajectory due to the small current population size, estimated at ~1400 individuals from an aerial survey in 2017 (Watt et al. 2021).

*Corresponding author: biddlecb@myumanitoba.ca

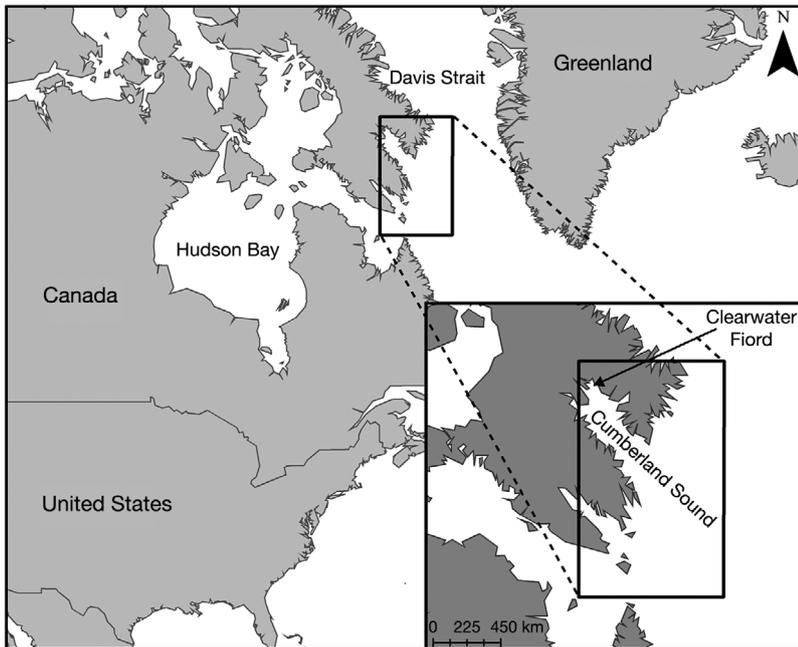


Fig. 1. Delineation of Cumberland Sound study area used to clip raster files

Population assessments are an important aspect of species population management because they allow population changes to be monitored over time, providing the opportunity to mitigate those changes if necessary. Stock production models are a common way of assessing fisheries abundance (Pella & Tomlinson 1969, Horbowy 1996, Marcoux & Hammill 2016, Hilborn et al. 2020). A stock production model analyzes various types of demographic information from a population to determine changes in abundance from harvest and to project future abundance (Maunder & Punt 2013). Stock assessment models are used for monitoring aquatic populations because even if data are lacking, models can still be created using available information such as catch history, which often has well-kept records (Maunder & Piner 2015, Best & Punt 2020).

Marine mammal population assessments began utilizing techniques from fisheries stock production models in the 1960s, because previous management methods were resulting in rapid declines of many cetacean populations (Wade 2018). Although the structure is similar, the terminology and output goals for fisheries versus marine mammal stock production models differ to reflect their different goals. In fisheries, stock production models function primarily to provide biological reference points to inform quotas and identify overfishing in stocks (Hilborn & Walters 2013, Wade 2018). For marine mammal applications, stock production models are altered to calculate

parameters such as removal level, pre-exploitation population size, or maximum net productivity level (MNPL) and have become an effective way to utilize commonly available data to address cetacean population dynamics (Baker & Clapham 2004, Wade 2018). Stock assessment models for both fisheries and marine mammals can be altered to include more detail, such as sex and age data (Hilborn & Walters 2013, Mosnier et al. 2014), but for many marine mammal populations, these types of data are lacking. While a large amount of information about a population's past, present, and future can be gained from stock production models, they often do not incorporate other biotic and abiotic aspects of the ecosystem that are potentially important determinants of population dynamics. Typically, these variables are ignored for many species because of a

lack of data on the relationship between environmental change and population dynamics (Maunder & Piner 2015).

The CS beluga population has been modelled previously using a Bayesian state-space model, informed by historical harvest data and aerial survey data (Watt et al. 2021). The impact of various harvest levels was assessed by calculating the probability of population decline in 10 yr. Within a management framework, predicting the effect of various harvest scenarios on the probability of population decline is considered a risk-based approach and is appropriate for evaluating populations that are considered data rich. Data rich in this context is defined as having 3 or more abundance estimates within a 15 yr period (Stenson & Hammill 2008). This approach allows those involved in population management to make decisions based on the risk of decline they deem appropriate. Potential biological removal (PBR) is another method for addressing management objectives, focused on quantifying the number of animals that can be removed from a stock while allowing a stock to reach or stay at its MNPL after 100 yr (Wade 1998). Using the risk-based approach, Watt et al. (2021) suggested that a harvest quota of 20 individuals would correspond to a 50% probability of population decline. The priors for this model were determined using traditional knowledge, previous cetacean models, and knowledge of cetacean ecology (i.e. Wade 1998, Marcoux & Hammill 2016). As

with many other cetacean population models (Wade 1998, Thomsen et al. 2011, Jacobson et al. 2020), the existing CS beluga model lacks detail due to many unknowns in beluga demography and did not consider how environmental change may be impacting the population. There are still many unknowns surrounding environmental effects on beluga whale survival and fecundity (Laidre et al. 2015). Previous cetacean knowledge can provide a basis of knowledge for population models, but the lack of reliable data impedes the inclusion of details, such as direct effects of an environmental variable on any population parameter, into current models. Although direct environmental effects are unclear, there is evidence suggesting that changing sea ice dynamics, and subsequent changes in food availability, will affect beluga whale body condition, and thus population size, through negative effects on survival (Laidre et al. 2008, Choy et al. 2020). Predicted effects are indirect, but there is value in including environmental effects in population models to garner a better understanding of population-wide effects.

Arctic marine ecosystems have undergone rapid change over the past 4 decades (Comiso 2012, Singh et al. 2013, Parkinson 2014). Climate change has contributed to a 4.7% decline in sea ice extent per decade and a decrease of 5 d decade⁻¹ on average in the length of the sea ice season across the Arctic (Comiso 2012, Parkinson 2014, Yadav et al. 2020). Accompanying the loss of sea ice has been a general increase in sea surface temperature (SST) in all regions north of 60°N (Singh et al. 2013). These environmental changes are predicted to affect Arctic marine mammals, although the ability to predict the specific effects that environmental change will have on populations is limited (Burek et al. 2008, Laidre et al. 2008, Kovacs et al. 2011). Belugas are expected to be sensitive to climate change, influenced by stressors such as ice entrapment—triggered by rapid changes in weather, reduced availability of ice-associated prey, and increased predation pressure from killer whales expanding north (Laidre et al. 2008, 2012, Kovacs et al. 2011). Most of these predicted effects are indirect, and thus difficult to quantify, and relate to specific aspects of beluga population dynamics. The direct effects of sea ice data have been included in a population model for harp seals (Hammill et al. 2021), but compared to cetaceans, more data and thus more explicitly identified relationships between variables and population parameters are available for seals.

Several environmental variables that have been predicted to affect beluga populations, among them sea ice extent, are a recurring concern due to the

close association beluga whales have with sea ice (Laidre et al. 2008). Alongside accessing prey that inhabit under-ice areas, sea ice cover acts as refuge from killer whale predation (Shelden et al. 2003, Bluhm & Gradinger 2008). Due to these associations with ice, variations in sea ice cover affect beluga behaviour and have been predicted to affect survival (Kovacs et al. 2011). Sea ice in CS melts in the summer (Maslanik et al. 2011, Yadav et al. 2020), so to understand the relationship between sea ice and beluga whales, sea ice concentration (ICE) values in winter are more ecologically relevant. In contrast, summer months do not accurately reflect the condition of the ice in a given year. Though studied less than ICE, SST is another important environmental variable in beluga ecology (Blix & Steen 1979, Aubin et al. 1990). SST impacts beluga whales because warmer waters promote molting and the proliferation of new skin cells and are important for calf thermoregulation (Sergeant 1973, Blix & Steen 1979, Aubin et al. 1990). Calves are born with a thin blubber layer and thus benefit from a warmer habitat initially until they amass thicker, more insulating blubber. Colder-than-usual water in estuaries has been linked to decreased survival of beluga calves (Blix & Steen 1979), though this relationship remains understudied. Conversely, increased SST caused by climate change has been predicted to depress calf survival rates, especially alongside other stressors such as reduced prey biomass and increased environmental contaminants (Williams et al. 2021). Both molting and calving occur in the summer months, so fluctuations in summer SST are likely to have an impact on beluga whales. ICE and SST can have short- and long-term impacts on beluga populations (O’Corry-Crowe 2009, Kovacs et al. 2011). Due to sea ice’s connections to refuge from predation, declining sea ice is predicted to have short-term effects on mortality; long-term effects are more likely to relate to prey availability (such as the cumulative effects of limited prey consumption) and be difficult to predict (Laidre et al. 2008). Recent research suggests that changing sea ice dynamics are already affecting belugas through reduced body condition connected to reduced prey availability (Choy et al. 2020). The short-term effects of SST are likely related to calf thermoregulation, as a year with unusually low or high summer temperatures could affect calf survival and thus have immediate effects on population dynamics (Blix & Steen 1979, O’Corry-Crowe 2009). SST also affects beluga molting (Aubin et al. 1990); low temperatures may inhibit molting and cell proliferation, potentially affecting abundance through reduced body condition, but unsuit-

able conditions may need to be prolonged before there are notable population-wide effects.

The objective of this study is to incorporate environmental covariates, specifically ICE and SST, into a stock production model to include the effects of environmental variation on estimates of CS beluga population trends. Further, we aim to compare models with and without covariates to determine how the inclusion of environmental variables might alter predicted future trajectories and thus population management plans.

2. MATERIALS AND METHODS

2.1. Model specification

The CS beluga stochastic stock production model from Watt et al. (2021) was used as a template to incorporate the effect of environmental covariates on population dynamics (Fig. 2). The model was structured with density dependence acting on population

growth rate fit to aerial survey data from 1990 to 2017 and harvest history from 1960 to 2017 using Bayesian Markov chain Monte Carlo (MCMC) methods to estimate population dynamics from 1960 to 2017. In this hierarchical state-space model, data are considered to be the outcome of 2 distinct stochastic processes: a state process and an observation process (de Valpine & Hastings 2002). The state process arises from underlying population dynamics and evaluation of stock size over time and is a discrete formulation of the Schaefer (1954) model, which allows both positive and negative effects on growth rate. The state process uses population parameters and error (quantifying random variation in population dynamics) to estimate true population size annually. Population size, N_t , is a function of the previous year's population:

$$N_t = N_{t-1} \times \left[1 + (R_{\max}) \times \left(1 - \frac{N_{t-1}}{K} \right) \right] \times \varepsilon_p - R_t \quad (1)$$

where R_{\max} is the maximum growth rate or rate of population increase; K is the environmental carrying capacity; ε_p is a stochastic term for the process error with environmental covariates; and R_t is the removals for that year, calculated as reported catches, CR_t , that are corrected for the proportion of animals that were struck and lost, S&L:

$$R_t = CR_t \times (1 + S\&L) \quad (2)$$

S&L is also a way to account for potential under-reporting in catch history. S&L data themselves can be under-reported, but because we have no available S&L data for CS belugas, we must rely on the prior being informed by data from eastern Hudson Bay belugas (see Watt et al. 2021).

The observation process is the relationship between true population size (N_t) and observed data (S_t), associated with random uncertainties, or observation error (ε_{S_t}), in data collection and abundance estimation. The logarithm of the median N_t estimate from this log-normal model is applied to the state process model described above.

$$\ln(S_t) = \ln(N_t) + \varepsilon_{S_t} \quad (3)$$

A model of this type would benefit from the inclusion of age or sex structure, especially considering one of our chosen covariates, SST, potentially has a differing effect based on age. Unfor-

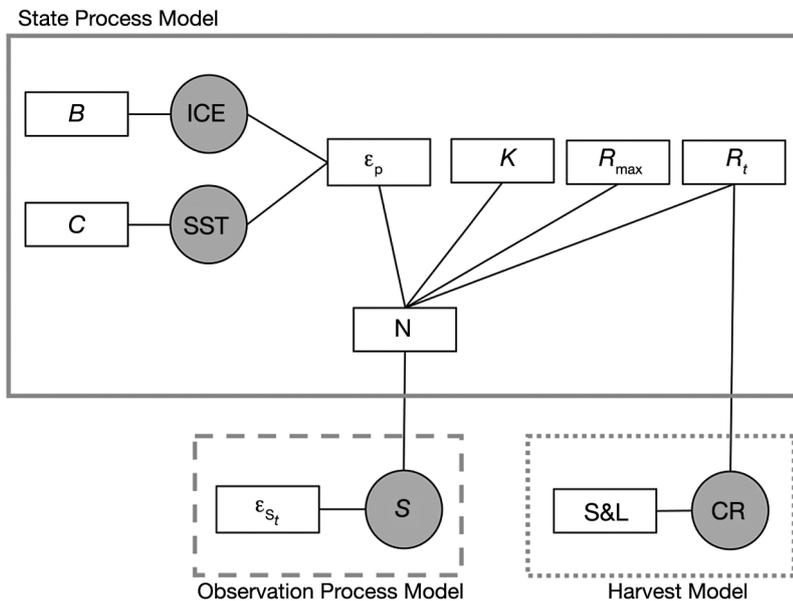


Fig. 2. Hierarchical state-space population model structure depicting linkages between state process (solid grey outline), observation process (dashed grey outline), and harvest (dotted grey outline). Grey circles indicate data, white rectangles indicate parameters to be estimated by the model, and black lines indicate dependencies between parameter and/or data. N : population size; R_{\max} : maximum growth rate or rate of population increase; K : environmental carrying capacity; ε_p : stochastic term for the process error with environmental covariates; R_t : removals for that year, calculated as reported catches (CR) that are corrected for the proportion of animals that were struck and lost (S&L); S : survey data; ε_{S_t} : stochastic term for observation error; ICE : mean sea ice concentration in Cumberland Sound (CS) in March; SST : mean sea surface temperature in CS in August; B : coefficient being estimated by the model for ICE ; C : coefficient being estimated by the model for SST

tunately, our model does not contain information on age or sex for this population, as there are no reliable data available at this time.

Included surveys occurred in 1990, 1999, 2014, and 2017; all surveys were systematic visual in design. All surveys were adjusted to account for availability bias, and the 2017 survey was adjusted for perception bias (as per Watt et al. 2021).

2.2. Process error incorporating environmental covariates

To capture more of the natural variation within the population, process error was modified from the previous template model to include the effects of environmental variation. ICE and SST were incorporated into the process error term (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n048p051_supp.pdf for details). Both ICE and SST are spatially gridded data with a $1^\circ \times 1^\circ$ resolution consisting of monthly averages and were obtained from the HadISST data set (Rayner et al. 2003).

The model requires the process error to have annual values for each covariate, so to avoid the loss of nuance in interannual variation, we chose to use a single month based on ecological significance to belugas, instead of an annual average. We used ICE data from March of each year from 1960 to 2018, as March, on average, is the month of highest sea ice extent across the Arctic (Maslanik et al. 2011, Stroeve et al. 2012). For SST, we used August data, as August, on average, is the month with the highest SSTs (Shea et al. 1992, Chambault et al. 2018). We chose ICE and SST maximum months *a priori* based on ecological relevance, but we also considered minimum months for either variable and intra-annual patterns in ICE and SST. Months with minimum ICE and SST values, August and March, respectively, were explored as well as the same month for both ICE and SST and annual averages. ICE values in August largely reflected a lack of ice cover, which was not valuable for representing environmental variation. SST values in March were not ecologically applicable to beluga whales, compared to summer months, as variability in SST was predicted to have the most impact on beluga whale summer ecology. We decided not to explore the use of minimum months further, as minimum ICE in August represents a time when sea ice cover has less ecological importance to belugas; in addition, minimum SST in March was too highly correlated with ICE in March (Pearson correlation coefficient of -0.97) to be considered independent of ICE.

Similarly, when the same months were tested for ICE and SST across the year, correlation remained high. Finally, annual averages were also tested, but using all the values within a year dampened the extremes in ecologically relevant months that we were aiming to investigate the effects of.

We used a 6×9 pixel polygon to extract data from the environmental raster files specific to CS (Fig. 1). The means of all pixels in the resulting clipped raster files from each year were calculated, and the mean values were translated into a z-score for ICE and SST separately. z-scores were used in the process error, so the environmental variables in the model reflected the variation of each value from the mean for all years during the study period of 1960 to 2018 (Fig. 3). We used a Pearson correlation test to determine if there was collinearity between ICE and SST and if they could be incorporated into the same model. The resulting correlation coefficient was -0.12 , which is low enough to allow for the incorporation of both environmental covariates into the model (Vatcheva & Lee 2016). We also tested the square of SST in initial model runs to determine if there was a non-linear relationship, where extreme highs and lows had a negative impact on population size. The inclusion of SST^2 decreased model fit and thus was not explored further.

2.3. Priors

The majority of priors remained the same as those in the template model (Table 1) from Watt et al. (2021). The stochastic process error term ϵ_p was altered to include the additive effects of ICE and SST. The equation below was used for the location parameter of the process error, with the precision hyperparameter (ϵ_{pr})

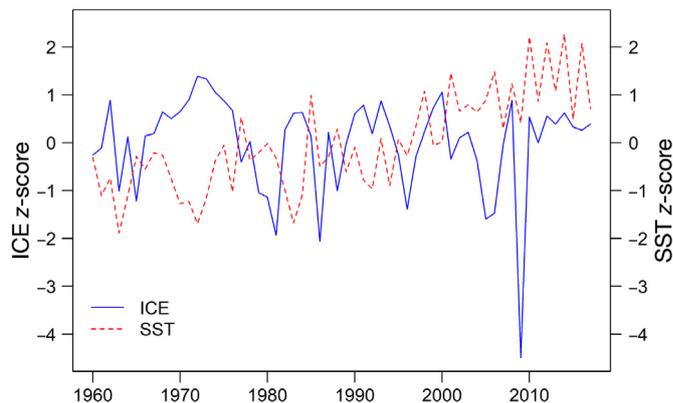


Fig. 3. Mean sea ice concentration (ICE) in March and mean sea surface temperature (SST) in August as z-score values in Cumberland Sound from 1960 to 2017

Table 1. Prior distributions, parameters, and hyperparameters used in the template population model (from Watt et al. 2021) and environmental covariates sea ice concentration (ICE) and sea surface temperature (SST) corresponding to the process error used in the final model. dist.: hyperparameter with its own prior distribution; (-) not applicable to the model

| Parameter | Notation | Prior distribution | Hyperparameter | Value from Watt et al. (2021) | Value for model with ICE and SST |
|------------------------------------|---------------------|--------------------|--------------------------------------|-------------------------------|--|
| Survey error (t) | ε_{S_t} | Log-normal | μ_s τ_s | 0 dist. | 0 dist. |
| Precision (survey) | τ_s | Gamma | α_s β_s | 2.5 0.4 | 2.5 0.4 |
| Process error (t) ^a | ε_{p_t} | Log-normal | μ_p τ_p | 0 dist. | $B \times \text{ICE} + C \times \text{SST}$ dist. |
| Precision (process) ^a | τ_p | Gamma | α_p β_p | 1.5 0.00005 | 1.5 0.001 |
| ICE coefficient ^a | B | Normal | μ_B τ_B | - - | 0 5 |
| SST coefficient ^a | C | Normal | μ_C τ_C | - - | 0 5 |
| Struck and lost | S&L | Beta | α_{sl} β_{sl} | 3 4 | 3 4 |
| Initial population ^a | N_{1960} | Uniform | N_{upp} N_{low} | 4000 1000 | 9000 1000 |
| Carrying capacity | K | Uniform | K_{upp} K_{low} | 15 000 2000 | 15 000 2000 |
| Lambda ^a | λ | Uniform | | 0.01–0.05 | 0.01–0.07 |

^aVariable differs from or is new to the template model

free to vary to account for error not explained by the covariates (see R code details in the Supplement for details).

$$(\varepsilon_p)_t = (B \times \text{ICE}_{t-1} + C \times \text{SST}_{t-1}) + \varepsilon_{pr} \quad (4)$$

where ICE is the mean concentration in CS in March, SST is the mean temperature in CS in August, B is the coefficient being estimated by the model for ICE, C is the coefficient being estimated by the model for SST, t is annual time, and ε_{pr} is the random error from the process precision parameter.

Both ICE and SST were multiplied by independent coefficients and were autoregressive to an order of 1 to allow the model to determine the effect each environmental covariate had on process error and thus population dynamics in the following year. We focused on 1 yr autoregressive effects, although it is ecologically plausible that these covariates may have effects over a greater time span, and this would be valuable to test in future models. Prior distributions for coefficients were informed by the necessity for coefficients to fall between -1 and 1 . Initial exploratory runs were performed with each covariate alone in the model and with both covariates together. The best fit model included both covariates, both

with coefficients assigned moderately informed normal (0, 5) distributions. The model was also re-run with each covariate individually to explore the effect of each covariate alone.

The stochastic process error term ε_p included in the state process equation (Eq. 1) was assigned a log-normal distribution with a location parameter set by the process error equation (Eq. 4) described above. The precision parameter for the process error term was assigned a moderately informative gamma(1.5, 0.001) distribution. The precision term within the precision parameter was reduced as compared to the precision parameter in Watt et al. (2021) to allow the opportunity for process error to increase and have more of an effect on interannual variation in the population trajectory. Precision for process error was high in the Watt et al. (2021) model because, as a long-lived species, beluga whales were not expected to exhibit a high amount of annual stock variation. We decreased precision to allow the model to explore more variation, to accommodate uncertainty surrounding the covariates. Initial runs of the model showed that the prior distributions for starting population and R_{max} in the template model appeared to constrain the posterior distributions. Both parameters had uniform distri-

butions in the template model, so the starting population distribution was widened to a uniform (1000–9000) distribution, and R_{\max} was widened to a uniform (0.01–0.07) distribution (Table 1). The updated starting population distribution allows space for the model to estimate a slightly higher population in 1960 if necessary. R_{\max} in the template model was informed by known rates of population increase in odontocetes, which can range from 0.02 to 0.06 (Wade & Angliss 1997, Wade 1998, Lowry et al. 2008), which also informed our prior.

2.4. Parameter estimation and model diagnostics

Posterior estimates for all parameters included in the model were obtained using a Gibbs sampler algorithm implemented in JAGS (Plummer 2003). RStudio (R Core Team 2020; version 1.2.5033, R version 4.0.2) packages R2jags (Su & Yajima 2015; version 0.6-1) and coda (Plummer et al. 2006; version 0.19-3) were used to examine the results. We used an MCMC simulation method and visually inspected trace plots to check the convergence of parameters. Initial runs of the code investigated model convergence, mixing, and autocorrelation within parameters. Model fit was determined using the diagnostics described below and the deviance information criterion (DIC), although DIC did not have a difference >2 between any of the models (Burnham & Anderson 2002), so other diagnostics assessing convergence were used preferentially.

We visually inspected Geweke plots to test for mixing within each chain and used the Geweke diagnostic test of similarity between different sections of the chains (Geweke 1996). The Brooks-Gelman-Rubin (BGR) diagnostic test was used to validate convergence between chains by comparing the width of the 80% credible interval (CI) of the chains pooled with the mean widths of the 80% CI for each of the chains individually (Brooks & Gelman 1998).

In initial model runs, we used 3 chains which had the number of iterations corrected to equal 10 000 after a burn-in of 6000 and thinning value of 30. Once a top model was determined, that model was run using 5 chains and 100 000 iterations after a burn-in of 60 000, with thinning maintained at 30.

2.5. Future projections and management scenarios

To predict stock trajectory and sustainable yield, the model was extended 10 yr into the future under 5

different management scenarios reflecting annual harvests of 5, 10, 20, 30, and 41 individuals. Although a 10 yr trajectory is relatively short, it was chosen because, ideally, harvest quotas for marine mammals are re-assessed every 5 yr. The current harvest quota is 41 individuals, and because CS belugas are endangered and not predicted to recover at the current quota (Watt et al. 2021), only harvests below the current quota were considered for projections. We explored how adding environmental covariates changed the probability of decline from the template model.

To continue the comparison of our model to the template model from Watt et al. (2021), we estimated PBR using a recovery factor (F_R) of 0.1 for a threatened declining stock (Hammill et al. 2017). The equation for the PBR threshold is:

$$\text{PBR} = N_{\min} \times 0.5 \times R_{\max} \times F_R \quad (5)$$

where R_{\max} is the maximum rate of population increase (the default value for cetaceans is 0.04; however, in our calculation, we used the R_{\max} estimated by the model), F_R is a recovery factor (between 0.1 and 1), and N_{\min} is the estimated population size using the 20th percentile of the posterior distribution resulting from the model or the 20th percentile of the log-normal distribution (Wade 1998) of the aerial survey estimate.

Animals that are harvested as well as those that are struck and lost (S&L), those that are not reported, and those with other sources of human-caused mortality are all included in PBR estimates; thus, we need to estimate total allowable landed catch (TALC), which is calculated as:

$$\text{TALC} = \text{PBR} - \text{S\&L} \quad (6)$$

where S&L is estimated in the model.

3. RESULTS

The final CS beluga model, adapted from Watt et al. (2021) (Table 2), included ICE for the month of March and SST for the month of August in CS from 1960 to 2017. Differences between results for the 3 models tested (ICE alone, SST alone, and ICE and SST together) were minimal. DIC and BGR values were not distinguishable, and convergence of all parameters was similar. Due to the similarities, model selection was led by Geweke diagnostic test results, where the z-scores for multiple parameters in the ICE and SST models were lower than those in models with the covariates alone. The focal update of our final model was the addition of environmental

Table 2. Model outputs for the Cumberland Sound (CS) beluga stock model from Watt et al. (2021) and our final model. The mean, SD, median (50th quantile [Q]), 25th Q, 75th Q, and 95 % credibility intervals (CIs; 2.5 % and 97.5 %) are given for the following model parameters and their priors: carrying capacity (K), Lambda ($1 + R_{\max}$), process error (process), survey precision (surv), starting population (startpop), struck and loss (S&L), and population size in 2018 (N_{2018}). Coefficients for sea ice concentration (ICE; B) and sea surface temperature (SST; C) are included in the final model output. \hat{R} is the Brooks-Gelman-Rubin statistic; values <1.05 indicate convergence of chains. N.eff is the number of effective chains after considering autocorrelation

| Model | Parameter | Mean | SD | 2.5% CI | 25 th Q | 50 th Q | 75 th Q | 97.5% CI | \hat{R} | N.eff |
|------------------------------|-------------------------|----------|----------|----------|--------------------|--------------------|--------------------|----------|-----------|--------------------|
| Watt et al. (2021) | K | 8233 | 3567 | 2907 | 5067 | 7875 | 11258 | 14607 | 1.001 | 5.00×10^5 |
| | K .prior | 8489 | 3752 | 2321 | 5238 | 8486 | 11730 | 14678 | 1.001 | 470000 |
| | Λ_{\max} | 1.03 | 1.01 | 1.01 | 1.02 | 1.03 | 1.04 | 1.05 | 1.001 | 130000 |
| | Λ_{\max} .prior | 0.03 | 0.01 | 0.01 | 0.02 | 0.03 | 0.04 | 0.05 | 1.001 | 5.00×10^5 |
| | Error.process | 1.00 | 0.01 | 0.98 | 1.00 | 1.00 | 1.00 | 1.02 | 1.001 | 413103 |
| | Prec.process | 30092 | 24521 | 2213 | 12231 | 23736 | 41112 | 93588 | 1.001 | 97000 |
| | Prec.process.prior | 29982 | 24439 | 2189 | 12115 | 23673 | 41061 | 93179 | 1.001 | 5.00×10^5 |
| | Prec.surv | 6.97 | 3.30 | 2.09 | 4.56 | 6.45 | 8.82 | 14.79 | 1.001 | 5.00×10^5 |
| | Prec.surv.prior | 6.25 | 3.95 | 1.04 | 3.34 | 5.44 | 8.28 | 16.06 | 1.001 | 370000 |
| | Startpop | 3077 | 537 | 2042 | 2667 | 3100 | 3519 | 3946 | 1.001 | 160000 |
| | Startpop.prior | 2499 | 867 | 1075 | 1747 | 2496 | 3252 | 3926 | 1.001 | 5.00×10^5 |
| | S&L | 0.38 | 0.16 | 0.10 | 0.25 | 0.36 | 0.49 | 0.72 | 1.001 | 3.00×10^5 |
| | S&L.prior | 0.43 | 0.18 | 0.12 | 0.30 | 0.42 | 0.55 | 0.78 | 1.001 | 5.00×10^5 |
| | N_{2018} | 1127 | 320 | 617 | 915 | 1090 | 1293 | 1864 | 1.001 | 450000 |
| Model with ICE and SST | B | 0.069 | 0.175 | -0.274 | -0.049 | 0.07 | 0.189 | 0.409 | 1.002 | 2300 |
| | B .prior | 0 | 0.447 | -0.876 | -0.301 | 0.001 | 0.302 | 0.876 | 1.001 | 5.00×10^5 |
| | C | 0.022 | 0.041 | -0.063 | -0.005 | 0.023 | 0.05 | 0.1 | 1.001 | 6300 |
| | C .prior | -0.001 | 0.448 | -0.879 | -0.303 | -0.001 | 0.301 | 0.874 | 1.001 | 5.00×10^5 |
| | K | 6730.256 | 3674.34 | 2283.076 | 3557.008 | 5666.034 | 9503.622 | 14394.33 | 1.001 | 290000 |
| | K .prior | 8496.225 | 3750.901 | 2324.527 | 5251.188 | 8494.387 | 11738.68 | 14679.03 | 1.001 | 5.00×10^5 |
| | Deviance | 77.942 | 2.662 | 74.056 | 76.069 | 77.494 | 79.349 | 84.336 | 1.001 | 32000 |
| | Λ_{\max} | 0.038 | 0.017 | 0.012 | 0.024 | 0.038 | 0.053 | 0.068 | 1.001 | 260000 |
| | Λ_{\max} .prior | 0.04 | 0.017 | 0.011 | 0.025 | 0.04 | 0.055 | 0.068 | 1.001 | 5.00×10^5 |
| | Prec.process | 1522.678 | 1225.991 | 125.019 | 627.594 | 1205.206 | 2080.094 | 4700.143 | 1.001 | 160000 |
| | Pprec.process.prior | 1501.998 | 1225.833 | 107.539 | 608.078 | 1183.907 | 2057.812 | 4678.578 | 1.001 | 410000 |
| | Prec.surv | 5.89 | 3.051 | 1.551 | 3.661 | 5.364 | 7.544 | 13.245 | 1.001 | 94000 |
| | Prec.surv.prior | 6.244 | 3.948 | 1.038 | 3.341 | 5.434 | 8.28 | 16.042 | 1.001 | 5.00×10^5 |
| | Startpop | 5210.593 | 2074.762 | 1667.14 | 3496.793 | 5147.265 | 6940.438 | 8779.238 | 1.001 | 120000 |
| | Startpop.prior | 5000.033 | 2308.343 | 1200.033 | 3001.54 | 5000.784 | 6994.66 | 8800.237 | 1.001 | 420000 |
| | Struck.and.lost | 0.407 | 0.17 | 0.111 | 0.279 | 0.397 | 0.526 | 0.755 | 1.001 | 1.00×10^5 |
| | Struck.and.lost.prior | 0.428 | 0.175 | 0.118 | 0.297 | 0.422 | 0.553 | 0.777 | 1.001 | 220000 |
| N_{2018} | 1344.081 | 568.566 | 564.362 | 973.792 | 1245.277 | 1591.109 | 2714.929 | 1.001 | 27000 | |

covariates, which resulted in updated variable estimates (Table 2). There was rapid convergence of all chains for carrying capacity (K), population size in 2018 (N_{2018}), process error, initial population size (N_{1960}), and S&L. Convergence of each chain was indicated by low autocorrelation in all variables (Fig. S1 in the Supplement) and a BGR statistic $\hat{R} < 1.05$ for all variables (Table 2).

The estimated maximum growth rate (R_{\max}) was 1.038, S&L was estimated at 1.40, and carrying capacity (K) was estimated at 5666. In 1960, the starting population was estimated at 5147 (95% CI 1667–8779), and the estimated value for N_{2018} was 1245 (95% CI 564–2715) (Fig. 4).

The coefficient for ICE (B) was estimated at 0.070 (-0.27 to 0.41), and the coefficient for SST (C) was

estimated at 0.023 (-0.06 to 0.10). These coefficients control the extent to which ICE and SST affect fluctuations in population trajectory. ICE and SST were translated into z-scores, so negative values reflect years below the mean and positive values reflect years above the mean for the study period. The positive values of both B and C mean that ICE and SST values directly affect the direction of population fluctuations. We also ran the model with ICE and SST separately (see the Supplement for model outputs). In both cases, the coefficients for ICE and SST remained positive, 0.002 and 0.013, respectively, but were lower than when both were included in the same model. Separate covariate models also resulted in less variation in the population trajectory over the study period compared to the final model (Fig. 5).

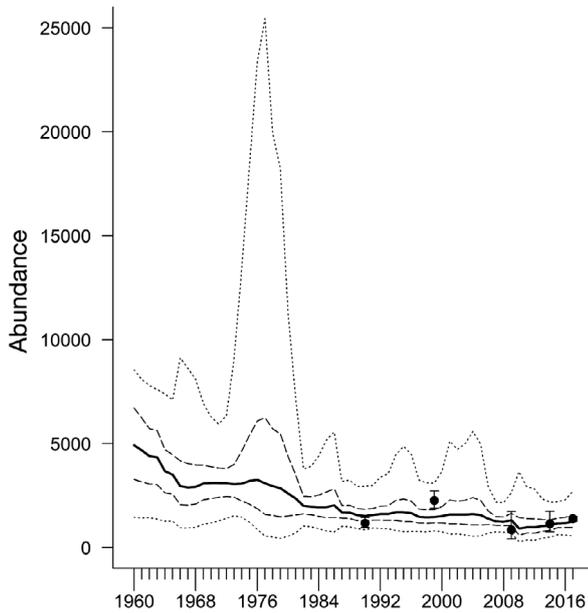


Fig. 4. Model estimates of Cumberland Sound (CS) beluga abundance fitted to adjusted aerial survey estimates flown in 1990, 1999, 2009, 2014, and 2017 (black dots \pm 95% log-normal credible interval [CI]) and harvest data from 1960 to 2017. Process error includes the effects of sea ice concentration and sea surface temperature in CS. Solid line shows the posterior median estimates, dashed lines show 50% CI, and dotted lines show 95% CI

To assess the impacts of different management strategies on the population, the model was used to plot the trajectories of 5 harvest scenarios (Fig. 6). The probability of population decline after 10 yr was 83% for a harvest of 41, 66% for a harvest of 30, 42% for a harvest of 20, 18% for a harvest of 10, and 9% for a harvest of 5 (Table 3, Fig. 7). Using the N_{2018} estimate from the model, the PBR was estimated at 2, and TALC was estimated at 1 individual.

4. DISCUSSION

The environmental variables ICE and SST were successfully incorporated into the stock production model for CS belugas. The covariates ICE and SST acted on the process error, impacting the CS beluga population trajectory by contributing to some of the variability in population dynamics. The positive coefficient for ICE means that following a year of above-average ICE, the beluga population would increase, and after a below-average year, the beluga population would decrease. Similarly, the positive coefficient for SST reflects an upward trend in beluga population trajectory following a year of above-average SST and a downward trend after a year of below-average SST.

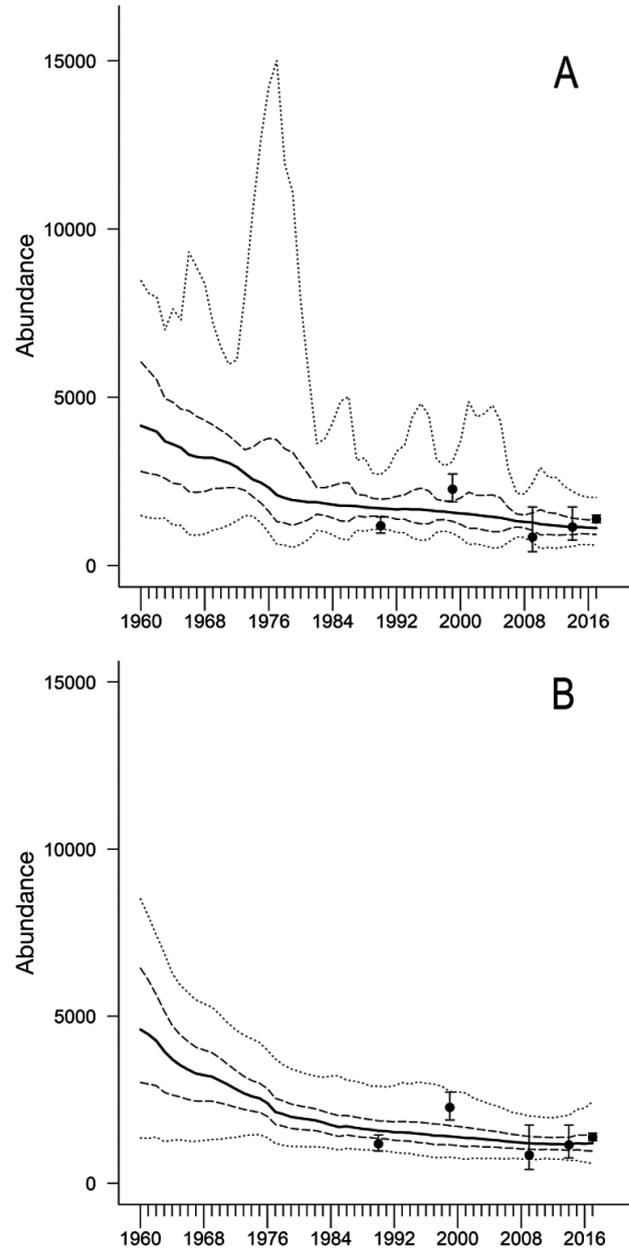


Fig. 5. Model estimates of Cumberland Sound (CS) beluga abundance fitted to adjusted aerial survey estimates flown in 1990, 1999, 2009, 2014, and 2017 (black dots \pm 95% log-normal credible interval [CI]) and harvest data from 1960 to 2017. (A) Process error with the effect of sea ice concentration in CS and without sea surface temperature. (B) Process error with the effect of sea surface temperature in CS and without sea ice concentration. Solid line shows the posterior median estimates, dashed lines show 50% CI, and dotted lines show 95% CI

The coefficients for both covariates are small, reflecting a relatively small effect that ICE and SST have on population trajectory indirectly through process error. Compared to abundance estimates from the template model (Watt et al. 2021), the largest difference in any

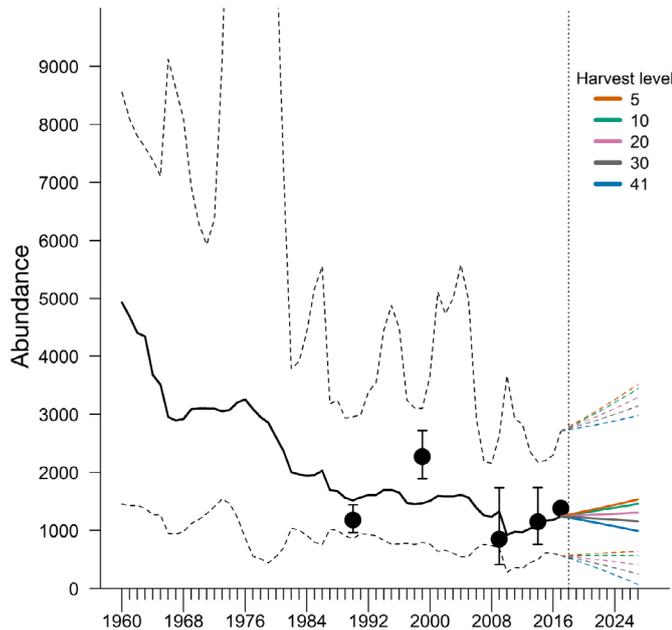


Fig. 6. Future population projections for Cumberland Sound (CS) belugas under 5 different harvest level scenarios based on population estimates from a stochastic stock production model including sea ice concentration and sea surface temperature, fitted to adjusted aerial survey estimates flown in 1990, 1999, 2009, 2014, and 2017 (black dots \pm 95% log-normal credible interval [CI]). Solid line shows the posterior median estimates, and dashed lines show 95% CI

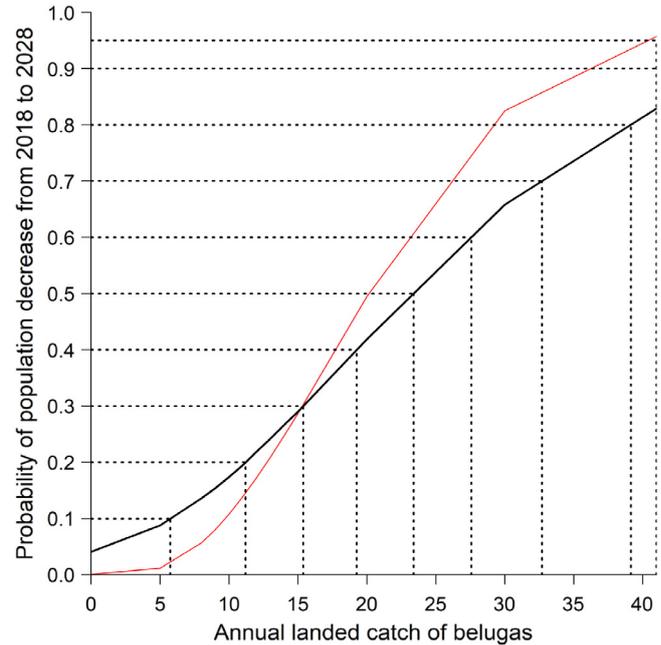


Fig. 7. Probability of the Cumberland Sound (CS) beluga stock decreasing from the 2018 abundance estimate after 10 yr of harvest, as a function of the number of reported belugas removed from the stock every year (black line). Dotted lines indicate levels of harvest (x-axis) corresponding to the probability of decline (y-axis). Red line shows probability of CS beluga stock decrease from template model (Watt et al. 2021)

Table 3. Probability that the Cumberland Sound beluga population, subjected to different levels of annual landed catch, will decline from the modelled 2018 population abundance estimate after 10 yr of harvest. Comparing results from Watt et al. (2021) and our final model (with sea ice concentration [ICE] and sea surface temperature [SST])

| Landed catch | p (%) Watt et al. (2021) | p (%) with ICE and SST |
|--------------|-----------------------------|---------------------------|
| 5 | 1 | 9 |
| 10 | 11 | 18 |
| 20 | 50 | 42 |
| 30 | 83 | 66 |
| 41 | 96 | 83 |

year was an increase of ~3000 individuals and the smallest was ~5 individuals. The greatest differences were in years at the beginning of the time series; this is likely because there are no available aerial surveys before 1990 to inform the trajectory, so during that period, the covariates have more power to inform trends.

Although the coefficients allude to ICE and SST having similar effects on population trajectories, ICE and SST have low correlation, so there is an interactive effect between these covariates and how they affect the CS beluga population. The coefficient for

ICE is 3 times larger than the coefficient for SST; therefore, in most years, ICE will have a greater effect on population fluctuations than SST. In years where the value for either covariate has a high deviation from the mean, that covariate had a stronger effect on population fluctuations. The greatest uncertainty in the population estimate is at the peak in the 97.5th quantile between 1970 and 1985. Aside from the lack of survey data in early years to bolster estimates, ICE trends were consistently high in CS in the early 1970s (Fig. 3), and based on the results from the models where covariates were included separately, it appears ICE is driving the majority of this uncertainty. Sea ice is inherently variable; despite clear downward trends, annual values are found to commonly deviate from the trendline (Cavalieri & Parkinson 2012). The quantiles for SST alone are smaller, with less variation. SST is potentially more stable over time than sea ice, which is seasonally dependent and susceptible to short-term fluctuations (Cavalieri & Parkinson 2012, Carvalho & Wang 2020). The combination of consistently above-average ICE values and relatively low harvest levels in the early to mid-1970s could have resulted in the model having increased uncertainty in population estimates for those years.

The final model contained both covariates, ICE and SST, but we also tested the independent effects of each covariate. While there was a positive effect from each environmental covariate on the model trajectory, similar to our final model, the coefficient was lower for both ICE and SST when they were separate. Although they have a notable effect on the population trajectory alone, when ICE and SST are considered together, coefficients for both are higher; thus, they have a greater effect on the re-creation of plausible population fluctuations, suggesting impacts are synergistic. There is also the potential that the larger effect for each covariate when they are together is the result of their more extreme values dampening the effects of each other, as they are not correlated, or the effect of an unknown confounding variable acting on both. It is difficult to identify other temporally variable covariates that have known effects on beluga whale population dynamics because although important habitat features have been identified (Laidre et al. 2008), the effect that changes in those features have on population dynamics has not been quantified. The overall trajectories of the separate models have shallower fluctuations than our final model. In the final model, the coefficients are greater and therefore have a larger effect on the process error and thus create more fluctuations in trajectory. The inclusion of both covariates is supported ecologically because there is likely interaction between these variables and how they are affecting beluga survival (Asselin et al. 2011, Hauser et al. 2017). Unfortunately, the data are still too sparse to identify these specific relationships in a population model context, but our model provides support that there is value in evaluating the interaction between ICE and SST and their effect on beluga populations, with the opportunity to expand on these relationships as additional data become available.

Multiple studies recognize that the environmental changes occurring in the Arctic are affecting beluga whales (Laidre et al. 2008, Kovacs et al. 2011), but identifying the specific connections to reproduction and survival is challenging. Belugas are highly ice associated; they prefer high ice cover (Asselin et al. 2011) and often use ice cover as refuge from predation (Stewart & Stewart 1989, Shelden et al. 2003). Declining sea ice can make beluga whales more vulnerable to predation and reduce access to prey (Heide-Jørgensen & Laidre 2004, Kovacs et al. 2011), which explains why our model determined that years of lower ICE had a negative effect on the CS beluga population trajectory. Beluga whales prefer to inhabit warmer water in the summer, as it is believed to

aid in skin molting (Watts et al. 1991). Calving also occurs in the summer, and warmer water likely increases calf survival by aiding thermoregulation (Sergeant 1973, Blix & Steen 1979). The connection between warmer water and important aspects of beluga ecology could explain the positive relationship between SST and beluga population size determined by our model. There is a loose correlation between low SST years and higher ICE, although there is a lot of variability within this relationship (Hurrell et al. 2008), so the lack of correlation in our data between ICE in March and SST in August in CS is plausible.

Our model uses covariates that are 1 yr autoregressive and thus focuses on the short-term effects of ICE and SST. The model could be altered to consider long-term effects by increasing the number of years the model is autoregressive to, resulting in model outputs being affected by years further in the past. Changing the temporal aspect of the covariate inclusion provides the potential to show how ICE and SST (or other covariates) affect the population after more than 1 yr, which potentially varies from the initial impacts (Gilg et al. 2012). For example, low ICE may cause beluga whales to have reduced access to prey, but the result of a change in resources may not show up in the population for several years. Similarly, if summer SST is lower than average and negatively affects beluga molting, the effects tied to incomplete molting may take a number of years to become quantifiable or not even act on population parameters directly. At this time, a lack of data makes it difficult to speculate on the time frame over which impacts might occur. We started by evaluating a 1 yr time frame, but additional data may support increasing the time lag. Hammill et al.'s (2021) harp seal population model utilized mortality data to determine a 1 yr time lag for the effect that sea ice anomalies had on the survival of young of the year. Our model could be updated with a specific time lag relationship of this nature once more data are available.

The inclusion of environmental covariates into our model resulted in changes to multiple aspects of the previous CS beluga model from Watt et al. (2021). In comparison to the template CS stock production model (Watt et al. 2021), the model presented here had a higher starting population estimate, a slightly higher N_{2018} estimate, and a lower carrying capacity. The maximum growth rate increased slightly toward the accepted default for cetaceans (Wade 1998), and S&L increased by 3%. In the template model, the population decrease over time followed a relatively linear trajectory. However, in our model, there are more noticeable peaks and troughs in the popula-

tion trend and wider CIs. The resulting increased starting population created a previously unobserved trend of steep population decrease early in the study period when both ICE and SST were below average for many years. This steep trend suggests that when the population abundance was higher, it was quite vulnerable to environmental fluctuations. The higher starting population also suggests that pre-harvest abundance is potentially higher than was suggested in Watt et al. (2021), although carrying capacity is estimated to be lower by ~2000 individuals. These differences may need to be considered for future management goals if density dependence were to act on the population as it approached carrying capacity; however, this is unlikely given its current population trend and endangered status (COSEWIC 2004).

We used a risk-based model approach to determine the probability of population decline under potential management scenarios. Compared to similar risk-based results from Watt et al. (2021), the inclusion of environmental covariates decreased the probability of decline for the 3 highest harvest scenarios and increased it for the 2 lowest scenarios. We speculate this is due to a more stable overall population trend in Watt et al.'s (2021) model (due to less variation in process error), allowing the population to remain stable at lower harvest levels. A lower 2018 abundance estimate from Watt et al. (2021) may cause high harvest levels to have a more dramatic effect, bringing abundance so low that population stability is lost. In the template model, a harvest of 20 had a ~50% probability of decline; in our model, a 50% probability of decline was reached at a harvest level of ~24. However, the recommended harvest suggested by our model is slightly more conservative than the harvest level suggested by Watt et al. (2021) when lower probabilities of decline are considered. Our model resulted in a 5% probability of decline over a 10 yr period, with a harvest of ~1, while Watt et al. (2021) found a suggested harvest of ~8 had a 5% probability of decline. Using the 2018 population estimate and the R_{\max} of 0.038 from our model, the PBR threshold was 2. The PBR threshold calculated by Watt et al. (2021), using their 2018 estimate and an R_{\max} of 0.04, had a value of 1. The slight difference between PBR thresholds is likely due to differences in estimated 2018 abundance. The goal of this work is to consider how environmental variables might change our interpretation of population trends and consider whether this ecosystem approach may be used for future assessments. In the face of uncertainty, a more conservative management strategy is beneficial because of the en-

dangered status of CS belugas (COSEWIC 2004). Further research using a Bayesian stock production model could provide clarity on the effects of environmental covariates on beluga population dynamics and provide increased confidence in sustainable management using a risk-based approach.

Hammill et al. (2021) proposed an age-structured harp seal population model with sea ice incorporated, where the specific relationship between sea ice cover anomalies and mortality of young of the year was defined. Compared to Arctic cetaceans, there are more data available on how covariates such as ice, which is used as a pupping platform, and prey availability affect specific aspects of harp seal population dynamics, such as mortality and reproductive rates (Stenson et al. 2020, Hammill et al. 2021). While the results of our model provide baseline knowledge on the effect of environmental variation on population fluctuations, there is the potential for the inclusion of much more detail in models of this type in the future, as ICE and SST are only 2 of many variables that may affect beluga population dynamics. Other relevant variables may include water depth, seafloor topography, and distance to important features such as shoreline (Asselin et al. 2011, Hauser et al. 2017). Belugas are thought to preferentially select for shallower water for increased prey availability; similarly, they select for regions with a higher seafloor slope, likely due to the increased productivity resulting from increased upwelling in these regions (Asselin et al. 2011). Suspected selection for these static habitat features may change depending on changes in dynamic features, such as ICE, and the interplay between habitat change, prey availability, and the presence of predators. This model could further benefit from the inclusion of predator and prey dynamics and the interactions these biotic variables might have with abiotic environmental variables. In this model, the environmental covariates were introduced via process error, yet as beluga whale research progresses, there is the potential for more specific relationships between beluga population dynamics and changes in environmental parameters to be quantified. An understanding of the mechanistic relationships would allow environmental covariates to be included into stock production models directly rather than within the process error, which would create more certainty in resulting parameter estimates. For example, if new data allowed us to quantify the relationship between ICE and mortality from predation, the model could be modified to include that direct relationship. ICE and SST impacted the CS beluga population trajectory; thus, inclusion of these variables in future models should be considered

to aid in explaining population trajectories of belugas and other Arctic marine mammals.

CS belugas are a threatened population under SARA (SARA 2017) and considered endangered by COSEWIC (COSEWIC 2004), and it is important to consider this status when making decisions on modelling, management, and conservation. Including climate and habitat changes that are affecting endangered species is important for conservation research because in many cases, climate change is shifting the baselines that guide conservation goals (Wilkening et al. 2019, Hirsch 2020). Many endangered species are specialists, endemic to their habitat, making them likely to be disproportionately affected as their habitat changes (Preston et al. 2008, Gough et al. 2015, Wilkening et al. 2019). A certain level of uncertainty is almost always involved in endangered species management (Gregory & Long 2009), but incorporating different types of data into population modelling has the potential to reveal sources of uncertainty that should be considered for more informed management of species at risk.

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