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# Eastern Hudson Bay Beluga <br> Precautionary Approach Case study: <br> Risk analysis models for comanagement. 

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Étude de cas de l'approche de précaution sur les bélugas de l'est de la baie d'Hudson: modèles d'analyse de risque pour la cogestion.

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#### Abstract

This case study attempted to develop modelling tools that would be useful in a co-management setting to develop a precautionary approach for the Eastern Hudson Bay beluga population. We developed and tested a stage-structured stochastic model that allowed the projection of population size over time given the uncertainty of population size and dynamics, and given management options involving a choice of hunting mortality and gender or age- (stage-) ratio of the catch. Uncertainty in initial population size was the single most important parameter in determining the uncertainty of projected population size over time. Projections were made over a period of 30 years. Risk was evaluated based on whether the population declined at any time during that period. Model runs showed that risk of decline was high if the population suffered hunt mortality in excess of a few tens of animals per year but a male-biased catch lessened this risk. At low population size, density dependence did not appear to matter to the risk probabilities.


## Résumé

Cette étude de cas avait pour but de créer des outils de modélisation utiles au développement d'une approche prudente pour la population de l'Est de la baie d'Hudson, outils qui doivent être également utiles étant donné le contexte de cogestion. Nous avons créé un modèle stochastique structuré par stages qui permet de projeter la taille de population dans le futur en tenant compte de l'incertitude de la taille initiale de la population et de sa dynamique de population, et selon les choix initiaux de gestion, choix qui comprennent l'ampleur de la mortalité due à la chasse et le ratio des sexes ou des âges (stages) des animaux. L'incertitude de la taille de la population initiale est le paramètre qui détermine le plus l'incertitude de la taille projetée de la population dans l'avenir. Des projections ont été effectuées sur une période de trente ans. Le risque était évalué en fonction de la probabilité de déclin de la population durant cette période. Les résultats de modélisation montrent que le risque de déclin est élevé lorsque la mortalité par la chasse dépasse quelques dizaines d'animaux par année mais qu'une chasse composée principalement de mâles a un risque plus faible. Lorsque la population est à un niveau faible, les effets de densité de population ne semblent pas avoir d'importance sur la probabilité de risque.

## INTRODUCTION

In 1998, a DFO national project was started to determine how the Precautionary Approach (PA) could best be implemented in the context of Canadian fisheries. To do so, a number of DFO researchers were asked to develop case studies of a variety of Canadian fisheries and exchange on them to ultimately recommend on a science approach to the precautionary approach in these fisheries. The underlying principle of the precautionary approach is illustrated by the quip: "When driving in the fog, drive slowly". In other words, when the status of a marine mammal hunt and the impact of further hunting are little known, be conservative and assume that there could be negative impacts.

The implementation of the PA in the context of aboriginal fisheries is a special case given the primacy of Inuit rights to wildlife resources afforded by the Constitution of Canada and reiterated by the Supreme Court. The usual premises of the precautionary approach (FAO 1996) that "all fisheries must be pre-approved" and that "the burden of proof of lack deleterious impact on the resource" rests on the users poses a problem. In Canada, the rights of aboriginal people to use wildlife resources cannot be limited without demonstrating reasonably that that use is contrary to conservation of those resources for themselves and others with rights on the same resource. The Canadian Government, as reiterated in the Sparrow decision, has the responsibility to act in good faith with aboriginal groups in ensuring that their rights are balanced against the conservation of the resource. Co-management, a system of resource management where aboriginal representatives and government share decisions, is the institutional instrument by which this can be achieved.

In the case of the E Hudson Bay belugas, it is our view that a risk analytical approach is conducive to co-management. The modelling approach allows the problem, its various parameters and their uncertainty to be presented in an explicit form that can be discussed by stakeholders. It allows multiple runs of the model, what-if experiments, to fuel discussion and inform decision-making. The model is not the answer by itself. The answer lies in the consensus that can arise from joint determination with users of the parameters of importance and their possible range of values and in the co-operative learning from joint inspection with users of the results of model runs. The answer also lies in the development of consensus on what amount of risk co-managers are willing to tolerate given the modelling that they did together with the modellers. We think that beyond the E. Hudson Bay the methods used here could be used to develop co-management precautionary approaches for other northern marine mammal stocks.

## METHODS

The models were developed on the software Analytica ${ }^{\text {TM }}$ for Windows, a risk analysis Monte Carlo programming environment (Lumina Decisions Systems www.lumina.com). This visual stochastic modelling software allows the creation of influence diagrams of model components. Each component or node (variables, decisions, objectives or limits) can be set, including its input parameter distribution, and the model can be run for set time periods. The software provides graphics and tabular methods of representing outcomes of the model or transition values of elements of the model at any point during the model run. It can also importance analysis of the each model parameter with respect to the model outputs. The models were designed to be stagestructured and gender-structured to allow the modelling of stage and gender-based management scenarios.

## Description of the basic stage-structured model

The motor of the stochastic model is a stage-structured population projection model (Crouse et al. 1987, Doidge 1990a, 1990b, Morin and Doidge 1992) which is described graphically in Fig. 1.


## neonate

young adult mature adult
Figure 1: Flow chart depicting a stage-structured population projection model
$P_{i}$ are the probability of individuals in stage $i$ surviving and remaining in the same stage; $G_{i}$ are the probabilities of individuals in stage $i$ growing and surviving to stage $i+1 ; F_{i}$ are the probability of individuals in stage i reproducing.
The model can also be described in matrix terms as follows:

$$
\begin{gathered}
N(t+1)=A \bullet N(t) \\
N(t)=\left[\begin{array}{l}
N_{1} \\
N_{2} \\
N_{3} \\
N_{4}
\end{array}\right]
\end{gathered}
$$

The population state vector at time $t+1\left(N_{t+1}\right)$ is the population state vector at time $t\left(N_{t}\right)$. Both vectors' elements are the numbers of animals in each stage at that time step.

The projection into each time step is done by matrix A which is:

$$
A=\left[\begin{array}{cccc}
P_{1} & 0 & F_{3} & F_{4} \\
G_{1} & P_{2} & 0 & 0 \\
0 & G_{2} & P_{3} & 0 \\
0 & 0 & G_{3} & P_{4}
\end{array}\right]
$$

where transition probabilities are actually calculated from basic stage parameter inputs:
The probability of surviving and staying in the same stage during a time step is:
$P_{i}=\left(1-p_{i}^{d i-1} / 1-p_{i}^{d i}\right) * p_{i}$
The probability of surviving and growing to the next stage by the subsequent time step is:
$G_{i}=p_{i}^{d i} *\left(1-p_{i}\right) /\left(1-p_{i}^{d i}\right)$
where $p_{i}$ is a constant within-stage annual survival and $d_{i}$ is a stage duration, " $i$ " is the stage index number. The probability of giving birth by the subsequent time step is $F_{i}$ and is equal to the crude birth rate (or the fecundity rate in the gender models). The matrix contains transition probabilities of stages over a time step. Each transition probability is a random variable defined by its probability distribution.

## Population size module

The population size at the start of simulation $\left(\mathrm{N}_{0}\right)$ is estimated by correcting the survey index $\left(\mathrm{I}_{0}\right)$ by the mean proportion $\left(\mathrm{P}_{0}\right)$ of time belugas tagged with satellite-linked time-depth recorders spent in the upper layers of water during the period of the survey. To this we added the total count made in the shallow waters of the Nastapoka estuary ( $\mathrm{N}_{\text {estuary }}$ ).
$\mathrm{N}_{0}=\left(\mathrm{I}_{0} / \mathrm{P}_{0}\right)+\mathrm{N}_{\text {estuary }}$
The uncertainty distribution of $\mathrm{N}_{0}$ is estimated by bootstrapping the uncertainty of the product or sum of these parameters. The estuarine count is assumed to be complete and is added to the outside population estimate. The module also contains a node that defines the start beluga stage proportions. These proportions are multiplied to the population size in the model at the start of simulation.

## Capture scenario module

The capture module of the basic is composed of three nodes: a 'Hunting scenarios' node, allows the user to select a specific level of hunting for each year of the projection and to do so under different hunting scenario; an 'Age capture ratio' node, allows the user to select a ratio of capture of each stage for each hunting scenario; a 'Captured each period' node is the result of the other two.

## Gender-specific model

In the gender specific version of the model, the stages are divided into an initial ratio of males and females ('initial gender ratio' node) and the harvesting scenarios are given a gender ratio ('gender
capture ratio by scenario' node). Accounting in all subsequent steps is done for males and females separately. This allows the user to explore the impact of gender biased hunts.

## Density dependent model

In the density dependent version of the model, the following formulas were used to apply a PellaTomlinsen modified logistic density dependent function to model parameters such as fertility, stage survival or stage duration as variables adjusted by the ratio of population size to carrying capacity.

$$
X_{N}=X_{N=K}+\left(X_{N=0}-X_{N=K}\right)^{*}\left[1-(N / K)^{z}\right]
$$

where:
N is the population size at a given time step.
K is the carrying capacity of the environment.
$X_{N}$ is the survival or fecundity parameter at population size $N$.
$X_{N=K}$ is the survival or fecundity parameter at population size $K . X_{N=K}$ is the minimum of the range of values for $X_{N}$.
$X_{N=0}$ is the survival or fecundity parameter when the population is close to zero.
$X_{N=K}$ is the maximum of the range of values for $X_{N}$.
$z$ is the shaping parameter of the density dependant function. It determines whether the density dependent function is a logistic (where $z=1$ ) or a modified (right skewed) logistic (e.g.: $1<z<$ 13.5).

A more intuitive explanation of the shape parameter is given by:
$z=\ln 0.5 / \ln \rho$
where: $\rho=N / K$ when the parameter changed by density dependence has varied half of its range, e.g.: $\rho=0.5$ when $z=1$ (logistic) and 0.95 when $z=13.5$ (heavily right skewed modified logistic) which means that the mid-range of parameter's values is reached when $\mathrm{N}=0.5 \mathrm{~K}$ in the former case and at $\mathrm{N}=0.95 \mathrm{~K}$ in the latter case. Rho, $\rho$, is used as the input shape parameter rather than $z$ because the former is easier to explain in terms that people understand, i.e.: N as a proportion of K.

## Parameters for modelling the E. Hudson Bay population

In some cases, model parameters have been estimated for the Eastern Hudson Bay stock of belugas (Doidge 1990, Kingsley 2000). In other cases, we had to use subjective assessments based on expert knowledge or analogies with other stocks of belugas or other species. This is particularly true of the uncertainty distribution of many of these parameters. Because there are no long-term studies of vital rates of belugas, we used estimates on time-variance from other species of marine mammals where there have been long term studies, whose results have been published. The estimation methods for time variance and estimates are given in Appendix I.

The choice of parameters used in the modelling are the result of a workshop held between the authors in Kuujjuaq on 21-22 February 2000 (Table1). The population index, $\mathrm{I}_{0}$, at start of modelling was the mean estimate of the published 1993 offshore survey (Kingsley 2000). The uncertainty distribution for the offshore estimate was the Lognormal distribution evaluated from the mean and standard deviation of this estimate. The parameters of the Lognormal in Analytica ${ }^{\mathrm{TM}}$ are defined by the median and geometric standard deviation. These were calculated from the survey mean and standard distribution using methods given by Strom (2000) and Strom and Stansbury (2000). The index, $\mathrm{I}_{0}$, was adjusted by dividing it by the mean proportion near surface ( $<4 \mathrm{~m}$ ) and therefore likely to be seen during the survey period. We used the Normal for the uncertainty distribution and evaluated it for the mean and standard deviation of this estimate. To the adjusted
population size, $\mathrm{N}_{0}$, we added shore counts for estuaries used by belugas. These estuaries were not covered by the survey. As an uncertainty distribution, we used a Uniform distribution with the minimum and maximum counts during the period.

The stage durations, $\mathrm{d}_{\mathrm{i}}$, derived from Doidge (1990) were assumed to be invariant in this modelling exercise. The fecundities are also from Doidge (1990). We used a Normal distribution to model time-variance in fecundity. Estimates of time variance of fecundity do not exist for belugas but they can be derived from other species of cetaceans for which there are long term studies of individual fecundity. The formulas used for calculations and the results are given in Appendix I. Note that we were not convinced that time-variance of fecundity was quite so high for this beluga population. The rates calculated in Appendix I were based on cetacean populations that are suffering from anthropogenic impacts and these populations were probably higher in size relative to carrying capacity than the Eastern Hudson Bay stock. Nevertheless, they were used for want of alternatives. They should be considered pessimistic.

Constant within-stage annual survival, $\mathrm{p}_{\mathrm{i}}$, have been estimated by Doidge (1990) but such rates result from the effects of hunting mortality and natural mortality factors. With a range of fecundity estimates of 0.13-0.18, Doidge had obtained rates of increase $\lambda=0.96-0.97$. We therefore turned to the only estimate of a rate of increase from an unexploited beluga population that had previously been depleted by hunting. The St.Lawrence beluga population rate of increase was estimated at 1.02-1.03 (Kingsley 1998) but there were concerns that its growth could be impeded by health effects of accumulated pollutants and therefore may not reflect the full potential of beluga population growth. The maximum rates of increase that are normally assumed for odontocetes, at low population size are 1.03\%-1.04\% (Kingsley 1989, Reilly and Barlow 1986, Wade 1998). To simulate natural mortality only, using the fecundity parameters in Table1, we adjusted the survival rates to obtain approximately $\lambda=1.035$ on average. Survival parameters to achieve this mean growth rate were modelled after estimates from long term studies of killer whales, Orcinus orca, (Olesiuk et al 1988) and bottlenose dolphin, Tursiops truncatus, (Wells \& Scott 1988). Our choice of uncertainty distribution for survival estimates was the Uniform because the shape of that distribution is unknown and the distribution of survival rates must by definition be bounded between 0 and 1. The bounds of the uniform were selected by analogy to estimated time variance from Orca and Tursiops (Appendix).

| Parameter | Mean or most likely | Uncertainty distribution | Uncertainty parameters | Comments |
| :---: | :---: | :---: | :---: | :---: |
| $\mathrm{N}_{\text {estuary }}$ | n/a | Uniform | Range $=0$ to 148 |  |
| $\mathrm{I}_{0}$ : offshore index | 1014 <br> (or median = 936) | Lognormal | $\begin{aligned} & \hline S D=421 \\ & \text { (or geom stdev = 1.49) } \end{aligned}$ | Kingsley 2000 $N o=\left(I_{0}{ }^{*} P_{0}\right)+N_{\text {estuary }}$ |
| $\mathrm{P}_{0}=$ Proportion $\leq$ 4 m from surface | 59.1\% | Normal | SD= 4.12\% | August dive data of EHB belugas (Hammill unpubl.) |
| $\mathrm{d}_{\mathrm{i}}=\text { stage }$ duration | $1,5,16,17$ years for the four stages (*) | none |  | based on Doidge 1990 |
| $\begin{aligned} & \hline \mathrm{p}_{\mathrm{i}}=\text { constant } \\ & \text { within-stage } \\ & \text { annual survival } \\ & \hline \end{aligned}$ | n/a | Uniform | Min: $0.65,0.92,0.96$, 0.88; Max: 0.85, 1, 1, 1 for four stages | Based on analogy to Orca and Tursiops and assumption that $\lambda=1.35$ |
| Age distribution at start | 0.088, 0.267, 0.456, 0.189 for the four stages (*) | None |  | Stable age distribution set by initial runs of the model |
| Fecundity | 0.165 young adult 0.092 old adults | Normal | $\begin{aligned} & \text { SD= } 0.0494 \text { young adult } \\ & S D=0.0277 \text { old adult } \end{aligned}$ | Doidge 1990; SDs assuming CV 30\% based on Orca and Tursiops analogies |
| Age ratio of catch | 0, 0.011, 0.64, 0.349 for the four stages (*) | None |  | Doidge (unpubl.) |

Table 1: Parameters used in population models

* Note: stages are: newborn, juvenile, young adult and old adult


## Importance analysis

Models were subjected to importance analysis to assess the importance of uncertain parameters on model outputs. The makers of Analytica ${ }^{\mathrm{TM}}$ describe importance analysis as follows:
"Importance is the absolute rank-order correlation between the sample of output values and the sample for each uncertain input. It is a robust measure of the uncertain contribution because it is insensitive to extreme values and skewed distributions. Unlike commonly used deterministic measures of sensitivity, it averages over the entire joint probability distribution. Therefore, it works well even for models where the sensitivity to one input depends strongly on the value of another." (Lumina Decision Systems, Inc. 1999).

## Resampling algorithm sample size and model output

Because survival and fecundity parameters were set to be resampled at each time step (1 yr), the model behaved like a Markov Chain Monte Carlo projection. The model was run for 30 years, using a Median Latin Hypersquare resampling algorythm and a sample size of 500 samples per time step. Analytica ${ }^{\mathrm{TM}}$ was set to produce probability bands of the population size to summarise the raw output.

## RESULTS AND DISCUSSION

## Importance analysis

Results of the importance analysis show that uncertainty in the initial population index is responsible to a large extent for the uncertainty of model outputs (projected population size at time $\mathrm{t})$. At the first time step, not surprisingly, the correlation is very high (0.98) but it diminishes to 0.41 after ten years as the uncertainty of survival and fecundity parameters are resampled at every time step (1 yr) are compounded with time (Fig. 1). Nevertheless, the importance of the population index parameter remains large throughout that time period, relative to all other uncertain parameters.


Fig. 1: Rank correlation of parameters to model output (population size at time t) after ten years.

Clearly, the imprecision of survey estimates is the most serious impediment to making precise projections into the future of this stock under various management options. A precautionary approach based on prudent management choices will be largely driven by this imprecision, much
more than any other parameter. Consequently, future research efforts to reduce this imprecision would greatly help to narrow the probability bands of projected population numbers, more than research on any other model parameter. The proportion of time spent near surface ( $<4 \mathrm{~m}$ ) and the survival rates are second in importance but far less correlated to model output (0.06). The former is an area where data can be improved but this may not improve the variance of the proportion since that variance reflects individual behaviour as well as sampling error. Improving the latter would require the estimation of survival rates, a task which is generally considered difficult, if not impossible, because it would require a fairly large annual sample as well as estimates of the rate of population increase. The uncertainty of the estuarine counts may or may not be reduced by having simultaneous counts in the estuaries during the next survey, depending on beluga behaviour at the time. The time-variance assumed for the fecundity parameter (Appendix I) appeared high to us, as stated earlier, and may be unnecessarily conservative but it would very difficult to estimate timevariance in fecundity without considerable female reproductive sampling on a population which cannot suffer much harvesting. The alternative of doing long-term observations of marked individuals to determine the variation in individual calving is logistically impossible in Northern Quebec. In any case, this parameter is not correlated much with model output (0.03).

## Risk analysis

A choice of precautionary management options can be made if there are clear definitions of the outcome that is undesirable, over what time span, and what risk probability is considered unacceptable to co-managers. Except, to some extent, for the definition of undesirable outcome, these are in large part fishery management decisions, not strictly scientific questions. We have simplified for the purpose of demonstration by defining the undesirable outcome as being any decline in the population (i.e.: population growth rate<1) within a 30-year period. Thirty years seemed to be a useful time span because it is roughly the time span that most Inuk hunters of say 25-50 years of age will hunt in their life time and it is also a reasonable period to ask people to imagine in their mind.

## I. Basic model run

In the first run, we have not distinguished gender or modified stage-capture ratios. We simply varied hunting mortality. Risk probability in this case is determined by looking at the probability bands and determining the one where population growth is close to zero. Results suggest that, with no hunting mortality, the population would have a $100 \%$ chance of increasing (Fig. 2). With the stage-capture ratios that are presently observed in the Eastern Hudson Bay beluga stock (Doidge, unpubl.) and a hunting mortality of 30 animals, hunters would have a $<10 \%$ risk of causing a decline (Fig.3). Hunting mortalities for various hunting scenarios are given in Table 2.


Fig. 2: Probability bands of population increase over time given no hunting mortality.


Fig. 3: Probability bands of population increase over time given a constant hunting mortality of 30 belugas per year.

| Hunting mortality | Risk probability |
| :--- | :--- |
| none | 0 |
| 10 | 0 |
| 20 | $<5 \%$ |
| 30 | $<10 \%$ |
| 40 | $25 \%$ |
| 50 | $50 \%$ |
| 60 | $67 \%$ |

Table 2: Risk probability given a hunting scenario in the basic model

## II. Gender biased run

To estimate the difference in the risk probability, we used the gender-specific model and assigned a unbalanced gender ratio in the catch of 80:20 male:female. Results show a clear decrease in the risk probability (Table 3) compared to the basic model with no gender bias in the catch (Table 2).

| Hunting mortality | Risk probability |
| :--- | :--- |
| none | 0 |
| 10 | 0 |
| 20 | $<1 \%$ |
| 30 | $<1 \%$ |
| 40 | $1 \%$ |
| 50 | $5 \%$ |
| 60 | $10 \%$ |

Table 3: Risk probability given a hunting scenario in the gender-biased model
In other words, focussing hunting effort on males would be a more precautionary management strategy than a hunt affecting both genders equally. This is an extreme example (80M:20F) but it serves to illustrate the gain in sustainability from a male-focussed hunt. We assume here that there are no deleterious effects from depleting male numbers. If mature males are not equal in their contribution to reproduction, this assumption may not reflect their true value. Nevertheless, at present there is no evidence to suggest that the certain males in the population have an inordinate role in reproduction success.

## III. Density-dependent run

We have no data on the response of beluga populations to increasing density. So far in the risk analyses above, we have assumed that the population is far from carrying capacity and therefore little affected by density dependent responses in survival or fertility. To investigate the adequacy of this assumption, we chose an extreme example of density dependent response for marine mammals (Taylor and DeMaster 1993) by applying a logistic ( $\rho=0.5$ ) response function and an assumed carrying capacity (K) of 20,000 belugas. Based on initial runs of the deterministic version of the model, the following survival rate and fertility parameters at $\mathrm{N}=\mathrm{K}$ were chosen to produce a rate of increase on average equal to zero.

| Parameter | Mean or most likely | Uncertainty distribution | Uncertainty parameters |
| :---: | :---: | :---: | :---: |
| $\mathrm{p}_{\mathrm{i}}=$ constant within-stage annual survival | n/a | Uniform | Min: 0.65, 0.86, 0.96, 0.88 ; Max: 0.85, 0.94, <br> 1, 1 for four stages |
| $\mathrm{d}_{\mathrm{i}}=\text { stage }$ duration | 1, 6, 16, 17 years for the four stages (*) | none |  |
| Fecundity | 0.161 young adult 0.086 old adults | Normal | $\begin{aligned} & \hline \text { SD }=0.0483 \text { young } \\ & \text { adult } \\ & S D=0.0276 \text { old adult } \\ & \hline \end{aligned}$ |

Table 3: Parameters used in the density dependent run of the model at $\mathrm{N}=\mathrm{K}$

* Note: stages are: newborn, juvenile, young adult and old adult; changed parameters are bolded

Results of the density dependent model run are virtually identical to those without density dependence, supporting the assumption that, at the low population size, even strong density dependence does not significantly increase risk probabilities and an exponential growth model is an adequate approximation to estimate risk of decline.

| Hunting mortality | Risk probability |
| :--- | :--- |
| none | 0 |
| 10 | 0 |
| 20 | $<5 \%$ |
| 30 | $<10 \%$ |
| 40 | $25 \%<>33 \%$ |
| 50 | $50 \%$ |
| 60 | $67 \%$ |

Table 4: Risk probability given a hunting scenario in the density dependent model

## CONCLUSIONS

The first goal of our PA case study was to first develop tools to model the risk of management options given uncertainties in population size and dynamics. Simpler models could have been used, models that did not require so much information about population dynamics, but we wanted to be able to model stage- or gender-based management approaches. This was done successfully and initial model runs show that, for a population like the one surveyed in 1993, a hunting mortality of a few tens per year has a low risk of causing population decline if the gender ratio of the catch is even. Secondly, an uneven gender-ratio favouring males has an even lower risk of population decline.

Importance analysis showed that the uncertainty in population size was the single-most important factor in the uncertainty of projected future population size, more than any other uncertain parameter. Efforts to reduce this uncertainty would produce less diffuse projections and reduce risk in management. It is not certain that efforts to reduce the uncertainty of other parameters would help in reducing this risk. Finally, we were able to explore the consequence of density dependence, lending support to the assumption that a simple exponential growth model is adequate to estimate management risk at low population level relative to carrying capacity.

There remains to put these models to practice in the intended co-management setting so that decision makers can do what-if experiments with them when considering management options. In that respect, we had a small meeting with two hunter representatives following the abovementioned Kuujjuaq workshop. At that meeting, the model and its results were well received. They have yet to be tested in a larger co-management setting.

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## APPENDIX I

Time variance of survival and fecundity estimates cannot be estimated for lack of longitudinal studies from any beluga populations. All that can be done is to rely on estimates obtained from other species with similar life histories. Below I have estimated the variance of survival and fecundity rates drawing on longitudinal studies of known individuals of bottlenose dolphins (Wells and Scott 1988, orcas (Olesiuk et al. 1988) and humpback whales (Buckland 1988 and Clapham and Mayo 1988).

The total variance estimated from such data is composed of three variance components: the true time variance of the parameter and the sampling error. To remove the sampling error and estimate the true time variance, I have followed the methods of Link and Nichols (1994) (see also Hitchcock and Gratto-Trevor 1997, Kendall 1998, and Gould and Nichols 1998). The time variance (tausquared) was estimated as follows:

$$
\tau^{2}=\hat{\sigma}^{2}-\frac{1}{n} \sum_{i=1}^{n} \operatorname{var}(\hat{\phi})
$$

where the first expression (sigma-hat-squared) is the total variance of the parameter estimates and the subtracted expression is the mean sampling variance of parameter theta-hat. The covariance component described by Link and Nichols (1994) is zero when the estimates of annual life parameters are horizontal estimates, i.e.: based on individuals resighted every year (Seber 1982).

Estimates of time variance are given below in terms of coefficient of variation (or standard error/mean estimate):

| Parameter measured | CV | Years sampled |
| :--- | :---: | :---: |
| Orca survival time variance | $2.11 \%$ | 8 |
| Humpback survival time variance | $3.55 \%$ | 8 |
| Tursiops survival time variance | $1.60 \%$ | 8 |
|  |  |  |
| Orca birth rate time variance | $29.22 \%$ | 8 |
| Humpback fecund. time variance | $30.70 \%$ | 8 |
| Tursiops fecund. time variance | $27.95 \%$ | 8 |

The results are remarkably similar with survival CV estimates in the $2-4 \%$ and fecundity CVs around $30 \%$. These estimates are all based on 8 years of individual re-sightings so, in all likelihood, they may not have included extreme events in these stocks' history.


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