A population dynamics model and assessment of Bering-Chukchi-Beaufort Seas bowhead whales

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G. H. Givens*, J. C. George†and R. Suydam†

Abstract

We present a density dependent population dynamics model with a parameterization based on fecundity variables that can be independently empirically estimated. Using a baseline version of this model, we fit a population growth trajectory for Bering-Chukchi-Beaufort Seas bowhead whales using a time series of abundance estimates from ice-based surveys including the most recent in 2011 which provided a precise estimate of high abundance. Model projections begin in 1914, believed to correspond approximately to the lowest historical abundance of this stock. Unlike past assessments, our model fitting approach employs maximum likelihood techniques. Due to constraints and complexities in the model, maximization requires intensive sophisticated numerical techniques. The results indicate that there is little evidence for recent density regulation. Estimates of survival rates imply realistic age expectancies, and estimates of fecundity parameters imply strong reproduction. Discussion of the results includes strengths and weaknesses of our approach, comparison of our results with those from past analyses, and implications of our findings for population management.

1 Introduction

Here we describe a population dynamics model for assessment of the Bering-Chukchi-Beaufort Seas (BCB) stock of bowhead whales, *Balaena mysticetus*. Components of our model are based on the Baleen II model of de la Mare (1989), as described by Punt (1999), which is a surplus production model of the Pella-Tomlinson (1969) form. Like Baleen II, our model is age stratified, discrete time (in years) with density dependent reproduction. Our parameterization allows estimation of quantities for which there is direct independent observable evidence, reducing direct dependence on abstract quantities like a degree of density

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*Givens Statistical Solutions LLC, 4913 Hinsdale Drive, Fort Collins CO 80526, and Colorado State University, Fort Collins, CO 80523 U.S.A. geof@geofgivens.com. This work was supported by the North Slope Borough (Alaska) and the National Oceanic and Atmospheric Administration (through the Alaska Eskimo Whaling Commission).

†North Slope Borough, Department of Wildlife Management, Barrow, Alaska.
dependent compensation parameter. The technical specifications of our model are given in Section 2.

Our model is intended to facilitate the exploration of possible trends in biologically important parameters and therefore allows time dependent survival rates, age of first parturition and carrying capacity. We do not employ these features in our analyses here; those investigations are left for future work.

Our application is the assessment of BCB bowheads, so compared to Baleen II our model is specialized in the following ways:

• All whales age 1 and older (the ‘1+ population’) are subject to hunting (i.e., ‘recruited’).
• A step function is used to model the transition to sexual maturity.
• The sexes are pooled.
• Density dependence is driven by depletion of the age 1+ population.

Other significant departures from past modeling and estimation methods include:

• Survival is specified according to an age-dependent ‘survival curve’ which allows piecewise linear survival rates as a function of age; see below. Previous BCB bowhead analyses have applied a step function transition with a parameter indicating the transition age from one survival rate to the other. That parameter has been eliminated.

• Reproduction is parameterized by two parameters: the maximum biologically feasible and the maximum achievable population growth rates (at low depletion levels), where the former is the inverse of the minimum calving interval. This makes the maximum sustainable yield rate (MSYR) an output of the model.

• Unlike past work, population modeling begins in year 1914, which is believed to be approximately the year of lowest population size, rather than 1848, which marks the onset of commercial whaling and is the first year with recorded commercial catch.

• The model is estimated using a new maximum likelihood approach. This eliminates the need for Bayesian prior distributions, the use and selection of which have been strongly debated (e.g., Butterworth, 1995; Butterworth and Punt, 1995; Punt and Butterworth, 1999b; Givens et al., 1995a; Raftery et al., 1995; Givens and Thompson, 1996; Poole and Raftery, 2000).

• We incorporate the 2008 abundance estimate of Koski et al. (2010) and the 2011 estimate of Givens et al. (2014).
2 The bowhead model

2.1 Basic dynamics

The fundamental dynamics are

\[ N_{0,t+1} = 0.5N_{\geq pt,t+1}f_{t+1} \]
\[ N_{1,t+1} = N_{0,t}S_{a,t} \]
\[ N_{a,t+1} = N_{a-1,t}(1 - F_t)S_{a,t} \quad \text{if } 1 < a < c \]
\[ N_{c,t+1} = (1 - F_t)(N_{c-1,t}S_{c-1,t} + N_{c,t}S_{c,t}) \quad \text{if } a = c \]

where

- \( N_{a,t} \) = Number of whales of age \( a \) at the start of year \( t \).
- \( N_{\geq a,t} \) = Number of whales of age at least \( a \) at the start of year \( t \). (Half of these are assumed to be female.)
- \( p_t \) = Age of first parturition at the start of year \( t \). In our baseline model \( p_t = p \).
- \( F_t \) = Exploitation rate on \( N_{\geq 1,t+1} \). Hunting is assumed to be uniformly applied across all age classes except that calves are not hunted.
- \( S_{a,t} \) = Annual survival rate of whales age \( a \) during year \( t \). In our baseline model, we let survival be independent of time so \( S_{a,t} = S_a \).
- \( f_t \) = Pregnancy rate (calves per sexually mature female) during year \( t \).
- \( c \) = Age of oldest (consolidated) cohort. We set \( c = 50 \).

Also define

\[ \tilde{N}_{\geq a}(F) = \text{Number of whales of age at least } a \text{ at the start of a year, when the stock has equilibrated with constant catch rate } F \text{ and a time-independent survival curve, expressed as a fraction of the number of calves then. This is defined for } a \geq 1. \]
\[ \tilde{N}_a(F) = \tilde{N}_{\geq a}(F) - \tilde{N}_{a-1}(F). \text{This is defined for } a \geq 1. \text{Let } \tilde{N}_0(F) = 1. \]

2.2 Survival rates and stabilized ages

Next we establish survival and stable age distribution relationships. We adopt a piecewise linear vector of survival rates. The calf survival rate is \( S_{0,t}S_{m,t} \), then the survival rate increases linearly until age \( m \), at which point the survival rate is \( S_{m,t} \) thereafter. Specifically,

\[ S_{a,t} = \begin{cases} S_{a,t}S_{m,t} + aS_{m,t}(1 - S_{a,t})/m & \text{if } a \leq m \\ S_{a,t} & \text{if } a > m \end{cases} \]

Note that we treat \( m \) as time-independent for simplicity, but our general model can accommodate use of \( m_t \). With this approach the \( c + 1 \) parameters at time \( t \) represented by \( S_{a,t} \) are replaced by just three: calf survival rate (with a surviving mother) \( S_{0,t} \), mature survival \( S_{m,t} \), and age of reaching mature survival \( m \). Given the other parameters in the model, including \( S_{0,t} \) and \( S_{m,t} \), one can solve for \( m \) directly; see below.
The stable age distribution when the stock has equilibrated at a fixed hunting rate $F$ depends directly on survival rates. Since survival rates are time-independent when calculating the stabilized relative age indices $\tilde{N}_a(F)$, we can write

$$\tilde{N}_a(F) = \begin{cases} 
1 & \text{if } a = 0 \\
S_0 & \text{if } a = 1 \\
S_{a-1}(1 - F)\tilde{N}_a(F) & \text{if } 2 \leq a \leq c - 1 \\
S_{c-1}(1 - F)\tilde{N}_{c-1}(F)/(1 - S_c(1 - F)) & \text{if } a = c
\end{cases}$$

where time dependence of these terms is dropped for clarity (Punt, 1999).

### 2.3 Reproduction

For our baseline model the equilibrium pregnancy rate under constant catch rate $F$ is:

$$f(F) = 2\sum_{a=p}^{c} \tilde{N}_a(F)$$

and we may define the pre-exploitation equilibrium pregnancy rate as

$$f_{eq} = f(0).$$

Pregnancy rates depend on $f_{eq}$ and the following quantities:

- $f_{max}$ = The maximum theoretical pregnancy rate. This is also the inverse minimum calving interval.
- $A = (f_{max} - f_{eq})/f_{eq}$ = A resilience parameter.
- $z$ = A degree of compensation parameter.
- $\lambda_{max}$ = The theoretical maximum steady rate of population increase when the stock is very heavily depleted.

The importance of the latter quantities will become apparent below. Given the survival rates, $p_t$ and $\lambda_{max}$, one can derive $m$ by solving:

$$\arg \min_{m \in \{1, \ldots, c\}} Q(p_t, \lambda_{max}) = \arg \min_{m \in \{1, \ldots, c\}} \left\{ f_{max} \left( \sum_{a=p_t}^{c-1} \frac{1}{\lambda_{max}^{a+1}} \prod_{j=0}^{a-1} S_{j,t} + \frac{\prod_{a=p_t}^{c-1} S_{j,t}}{\lambda_{max}(\lambda_{max} - S_{c,t})} \right) - 1 \right\}$$

since the $S_{j,t}$ depend on $m$. Since $m$ is an integer, there are many values of $S_{j,t}$, $p_t$ and $\lambda_{max}$ that yield the same solution for $m$. Also, given $m$, the same equation can be used to obtain $\lambda_{max}$. In this case there is a single solution.

In our model, $\lambda_{max}$ is a parameter to be estimated, which has the effect of replacing MSYR in the parameterization. MSYR is calculable from the set of model parameters. This idea was advocated by Punt (1999) but not pursued in that paper.
2.4 Density dependence

To model density dependent fecundity, let:

\[
f_t = \max \{ f_{eq} \left( 1 + A \left( 1 - \left( N_{\geq 1,t} / K_t \right)^z \right) \right), 0 \}.
\]

where 

\[K_t = \text{Carrying capacity. In our baseline model } K_t = K.\]

The following quantities are useful for further understanding the dynamics:

MSYL = The population level at which the largest catch can be taken indefinitely without any change to the stock abundance.

MSYR = The sustainable catch rate achieved at MSYL.

\[\tilde{P}(F) = \text{The number of whales of age at least 1, when the stock has equilibrated with constant catch rate } F \text{ and time-independent survival rates, expressed as a fraction of the number of calves at pre-exploitation equilibrium.}\]

The difference between \(\tilde{P}(F)\) and \(\tilde{N}_{\geq 1}\) is the standardization constant. Now simplifying equations (19) and (20) of Punt (1999) yields

\[0 = 1 + \text{MSYR} \left( \frac{1 - \text{MSYL}^{-z}}{zf(\text{MSYR}) - f_{eq}} \right) \frac{df(F)}{dF} \bigg|_{F=\text{MSYR}}.\]

Equations (1) evaluated at \(N_t/K_t = \text{MSYL}\) and (2) constitute a system of two equations in two unknowns (\(z\) and MSYR). These may solved to derive those parameters given MSYL and the remaining parameters. This means that \(z\) and MSYR are calculable from other estimated model parameters rather than being directly estimated.

2.5 Starting conditions

The BCB bowhead population was very heavily depleted during commercial whaling starting 1848 and abundance may have reached a nadir in approximately 1914 (Bockstoce and Botkin, 1983; Bockstoce and Burns, 1993; Raftery et al., 1995). Although the early commercial catch data were painstakingly researched they clearly must be considered approximate. When fitting a model to the entire catch history, the region in parameter space that is strongly supported by the recent abundance data while remaining consistent with the long deterministic series of early catch data is extremely narrow. Informally, estimation must ‘thread the needle’. Thus we omit the early catch data to facilitate parameter estimation. This is similar to the practice of omitting early catch data when modeling the eastern north Pacific gray whale population dynamics because early catch data cannot be reconciled with recent observed abundances (Punt and Wade, 2012).

Our model begins in 1914 and is assumed to have a stable age distribution in that year. The number of whales of each age is given by:

\[N_{a,1914} = N_{a,1914} \tilde{N}_a(F_{1914}) / \sum_{j=0}^{c} \tilde{N}_a(F_{1914})\]
where $F_{1914}$ solves
\[
N_{1,1914} = 0.5N_0(F_{1914}) \sum_{a=0}^{c} \tilde{N}_a(F_{1914})
\]
and
\[
N_0(F_{1914}) = \left(1 - \frac{1}{A} \left( \frac{f(F_{1914})}{f_{eq}} - 1 \right) \right)^{1/\tau} \frac{K}{\tilde{N}_{1,1}(F_{1914})}.
\]
These latter two equations must be solved numerically for $F_{1914}$ before solving equation (3). See Punt (1999) for further details.

3 Estimation

3.1 Parameter estimation

We adopt the maximum likelihood paradigm for estimation. In our baseline model the parameters to be estimated are: $K$, $N_{\geq 0,1914}$, $S_0$, $S_m$, $f_{max}$, $\lambda_{max}$, $p$, and MSYL. Denote these by the vector $\theta$. With maximum likelihood estimates (MLEs) for those parameters, one can derive estimates for $m$, $z$, and MSYR.

The abundance data are abundance estimates and corresponding coefficients of variation (CVs) for the years listed in Tables 1 and 2 (compare to Zeh and Punt, 2005). Estimates for the years 2001 and earlier are slightly correlated because they share information about detection probabilities. Abundance estimates for 2004 and 2011 are independent of past estimates and each other because the 2004 estimate was derived from aerial survey data and the 2011 estimate provided entirely new estimates of detection probabilities. The catch data (which we write as $F_t$ for $t = 1914 \ldots$ present) can be obtained from the Secretariat of the International Whaling Commission (C. Allison, pers. commn).

The abundance data are expressed as log abundances, the standard errors of the logs (equated to the CVs of the abundance estimates for this purpose), and the correlation matrix of the logs. Denote the log abundance vector as $\hat{\beta}$ and the corresponding variance-covariance matrix as $\hat{\Omega}$. Note that the last two rows (and columns) of $\hat{\Omega}$ are zero (except for diagonal elements) due to the independence mentioned above.

These log data are assumed to be normally distributed with $\hat{\Omega}$ treated as known. The negative log likelihood function for $\beta$, is then given by
\[
- \log L(\beta_\theta) = 0.5(\hat{\beta} - \beta_\theta)^T \hat{\Omega}^{-1} (\hat{\beta} - \beta_\theta)
\]
where $\beta_\theta$ is the vector of projected log abundances in survey years from the dynamics model using parameters $\theta$. Thus, minimizing $- \log L(\beta_\theta)$ is equivalent to maximizing a corresponding log $L(\theta)$.

Maximizing the likelihood is not easy. There are three major challenges. First, some parameters of the model are constrained. For example, $S_0 \leq S_a$ for $a \geq 1$ and both these parameters must be between 0 and 1. Also the model (and common sense) require the
following constraints: $\lambda_{\text{max}} > 1$, $0 \leq f_t \leq 1$, $N_{t\geq 0,t} > 0$, $K > 0$, $0 \leq N_{t\geq 0,t}/K \leq 1$, $f_{\text{max}} \geq f_{\text{eq}} \geq 0$, $2 \leq p_t \leq 30$, $z \geq 0$, $0 < \text{MSYL} \leq 1$, and $0 < \text{MSYR} < 1$. Second, the likelihood function is highly multimodal; we discuss this further below. Third, the likelihood function is 8-dimensional but has high values mostly along a very narrow curved manifold in 8-dimensional space. Another way to say this is that the model is nearly over-parameterized: most of the information about the likely stock trajectory is given by abundance and productivity.

Due to these challenges, an intensive multi-stage optimization strategy was employed. Given a set of starting values $\theta_0$, we minimized $-\log L(\theta)$ with respect to $\theta$ using the strategy of cyclic coordinate descent (e.g., Givens and Hoeting, 2013). This approach holds all but one parameter (or a set of them) at the current best value while minimizing $-\log L(\theta)$ with respect to the remaining parameters. This provides an update for the chosen parameter. Then optimization is limited to the next parameter, holding all others fixed at their current values. We continue this procedure until all parameter estimates have passed a relative convergence criterion of 0.0001. In our application, we cycled over the parameter (sets): $(K,N_{t\geq 0,1914})$, $(S_0,S_m)$, $f_{\text{max}}$, $\lambda_{\text{max}}$, $p$ and MSYL. Brent’s (1973) method was applied for these minimizations, except for $p$ where we applied exhaustive search, and for the multivariate minimizations where we applied the Nelder-Mead strategy (see, e.g., Givens and Hoeting, 2013). The constraints described above were addressed by introducing various of log and logit transformations.

To cope with the near over-parameterization and multi-modality, we wrapped the above optimization strategy in the larger strategy of random starts local search (e.g., Givens and Hoeting, 2013). Simply put, this means that we repeated the above optimization process starting from many randomly chosen $\theta_0$ (and a few strategic ones). We used 3500 random starts. Many optima were found, and the many random starts yielded different but nearly minimal scores. Then we re-started optimization effort from each of the 10 best runs with a more stringent stopping criterion. This step proved unnecessary. From several of the best solutions found we used 50 additional random starts focused on uncertainty in survival rates and then, finally, took the maximum likelihood estimate $\hat{\theta}$ to be the value producing the minimum $-\log L(\theta)$ found during this entire exercise.

All this work might seem excessive, but consider Figure 1. Here, we plot $-\log L(\theta)$ as a function of $S_0$ while holding all other parameters fixed at their MLEs. The function has many local minima at different $S_0$ values quite near each other. Between these, other calf survival rates are poor. Moreover, during cyclic descent the shape of this function will change at each cycle. Such a function is a nightmare for applying standard optimization algorithms.

We use a profile likelihood ratio approach to estimate confidence intervals (Kalbfleisch and Sprott, 1970). To find an interval for, say, $S_0$, we began with the MLE $\hat{S}_0$ and the value of the likelihood at that point, holding all the other parameters fixed at their maximum likelihood values. We then identify all $S_0^*$ values for which the deviance $(-2 \times \log L(S_0^*) - 2 \times \log L(\hat{S}_0))$ does not exceed $\chi^2_{1,0.995} = 3.84$. This threshold is based on asymptotic properties of the likelihood ratio statistic (e.g., Casella and Berger, 2002). Since typical likelihood functions are smooth, unimodal and concave, the set of $S_0^*$ satisfying this criterion is usually an interval.
For our analysis, the likelihood function is much more complex and our approach can only be considered approximate. The horizontal dotted line in Figure 1 indicates the threshold, and points below the line are contained within the approximate confidence region. Here, the region is not an interval. In the two such cases ($S_0$ and $f_{max}$), the likelihood has an obvious underlying smooth shape with a few extremely narrow spikes. We approximated the confidence regions in these cases to enclose only the range corresponding to cutoffs for the smooth part. This introduces a very slight downward bias in confidence levels, but we believe that the improved interpretability is worth it and any bias is overwhelmed by the approximation inherent in our profile likelihood approach. In the case of MSYL, there is no underlying smooth shape—only a variety of spikes between 0 and 0.2. We avoid making a confidence interval for this case.

Our approach considers the profile likelihood function for each parameter separately. We make no attempt to identify joint confidence regions. If several parameter estimates are strongly correlated, then their joint confidence region may be much smaller than the box defined by the univariate intervals.

The parameters MSYR, $m$ and $z$ are calculated from other parameters rather than estimated directly. In principle, it is possible to determine 95% confidence regions for these parameters using the sampling distributions of the estimated parameters. In practice, this is impossible because the functional relationships between model parameters and these quantities are too complex. Instead, we use a very rough Monte Carlo strategy. We sample uniformly and independently one value from the range of each parameter’s 95% confidence interval, then use these sampled values to generate a value for, say, MSYR. This is repeated 100,000 times. We then adopt the range of MSYR values obtained as an approximate confidence interval. No attempt is made to infer a sampling distribution.

4 Results

Figure 2 shows the trajectory (red) produced by the MLEs. To gauge sensitivity and uncertainty, we also fit the model 13 times, in each instance omitting one survey from the dataset. These fits (black) produced very similar trajectories, except when omitting the 2011 estimate which is high and precise—and therefore influential.

Table 3 shows the estimated values for the parameters for the overall fit and the 13 cross-validation fits. Table 4 shows the MLE parameter estimates and corresponding 95% confidence intervals for the main analysis.

5 Discussion

This analysis is the first of its kind for bowheads. It is a full maximum likelihood analysis using a new model that replaces MSYR and $z$ with $f_{max}$ and $\lambda_{max}$. It proposes a new way to model survival rates. It ignores the early portion of the historical catch record to allow
a less constrained fit to the more recent data. It is highly generalizable so that it might be used to investigate time trends in survival, fecundity, or carrying capacity.

Our results open many questions. First, the results suggest that there is essentially no evidence for density regulation through 2011. In particular, the MLE for $K$ seems unbounded. It is not realistic that the western Arctic can support nearly unlimited whale numbers. However, we place a great deal of confidence in the accuracy and precision of the recent abundance estimates. Indeed, the remarkable population growth seen in the last two decades without signs of slowing is why density regulation has not been seen in the data. One possible explanation for our result is model misspecification. Specifically, our analysis uses constant carrying capacity, survival rates and reproduction. If there have been recent temporal trends in any of these variables, a model reflecting those trends might fit the data well while also allowing for density regulation. Future work investigating such possibilities is planned.

Second, the absence of information about $K$ raises the question of how one should interpret MSYL, MSYR and $z$. These quantities relate to depletion levels (relative to $K$), and if $K$ is virtually unlimited then depletion loses its meaning. Therefore, we avoid any interpretation and think of these parameters simply as nuisance variables or perhaps tuning parameters chosen to help the model fit the data (minimally, but more so in the cross-validation fits).

Third, our results give a false sense of precision. Our model is deterministic and is forced to produce trajectories that fit a very strong signal of abundance estimates in the most recent years. This strongly constrains the model, especially when the model must also be consistent with 100 years of historical catch data. Thus, we view our confidence intervals and point estimates as indicative of general areas in parameter space rather than impose a strict formal interpretation.

Fourth, our estimate of $f_{max}$ is too high. It implies a calving interval that could be less than two years. Realistically, bowhead biology suggests that two years is an absolute minimum interval and three years is probably more realistic. Another consideration relates to our above concern about unregulated productivity rates and the loss of interpretability of MSYR. Perhaps $f_{max}$ cannot be considered in isolation from the other parameters, especially $\lambda_{max}$.

Our estimated survival rates are fairly realistic, suggesting that a calf has about 11.5% chance of living to age 100 and 1.4% chance of living to 200 using point estimate survival rates. Whale ages have been estimated using a variety of methods (Lubetkin et al., 2008; George et al., 2011; Rosa et al., 2013; Wetzel et al., 2014) and 5.3% (12/225) and 0.4% (1/225) animals are believed to be older than 100 and 200 years, respectively. However, it is not possible to compare these percentages to our estimated probabilities because those empirical estimates are subject to hunting selection bias in favor of smaller (younger) whales in most villages. We can also compare our percentages to those implied by several earlier analyses. Using the results of Givens et al. (1995b), the survival percentages would be 13.1% and 2.1% for ages 100 and 200 respectively. The results of Punt and Butterworth (1999a, Table 10) would imply values of 18.3% and 4.5%, respectively. Brandon and Wade (2006) used a rather different assessment method, but the results from their work using a
methodology most similar to the others mentioned here would imply survival percentages of 24.1% and 8.0%. The latter numbers strain plausibility.

Our estimate of $P_{1914}$ (namely 1,114) is also reasonable. The estimate is high enough to provide at least some incentive to commercially hunt bowheads into the 1900s, yet low enough, together with the collapse of the baleen market at that time, to be a strong disincentive for commercial whaling (Bockstoce, 1986). The estimate of the nadir is consistent but in the low range of those posited by other researchers (Phillips et al., 2013; Woodby and Botkin, 1993).

The estimate of $p$ is remarkably close to the best estimate of the age at first ovulation reported by Rosa et al. (2013), namely 25.9 years. Bowhead gestation is a bit more than one year.

On the face of it our estimate for $\lambda_{max}$ is not unreasonable. The estimated growth rate in 2011 is 3.7% (95% confidence interval 2.8% to 4.7% (Givens et al., 2014)), and at lower population sizes it could have been higher as a fraction of abundance.

Finally, a notable feature of Figure 2 is the relative flatness—and even slight decrease—of the trajectory in the first 30 years. There are at least two reasons for this. First, as a fraction of estimated abundance, significant harvests were ongoing, sometimes exceeding 4%. Second, the model is initiated at a stable age distribution in 1914, and it may take some years for the age profile to shift to reflect contemporaneous dynamics.

5.1 Management implications

The BCB bowhead population is hunted by native Alaskan communities along the whales’ migration corridor. The current harvest rate is less than 0.4%, and recommended quotas are calculated by the Bowhead Strike Limit Algorithm developed by the International Whaling Commission (International Whaling Commission, 2003). The algorithm was developed and tested using a very large collection of simulation trials exploring how conservation performance and hunting need satisfaction depended on various scenarios including a variety of values for the parameters estimated here.

Our MLEs and confidence intervals for survival rates are well within the range of past testing. Generally speaking, our estimates for $K$ and the productivity parameters suggest a larger, more productive stock than was assumed during algorithm testing. For example, the values of MSYR tested were 0.01, 0.025, and 0.4, yet our analysis suggests that a value of 5.5% would not be implausible. The empirical estimate for current rate of population increase is 3.7%, yet our MLE for $\lambda_{max}$ suggests that the population is capable of even faster growth. Similarly, the MLE for $f_{max}$ is at the upper edge of what is biologically feasible. Not only does the stock appear to be highly productive, but our results also suggest that the carrying capacity of the region may be higher than previously believed and/or is increasing. This would explain why recent ice-based abundance estimates provide no indication of slowing growth.

Altogether, these results are reassuring in the sense that they provide no evidence that simulation testing of the Bowhead Strike Limit Algorithm was too precautionary. Our results
are consistent with the possibility that the set of tested scenarios was focused intensely on cases with nearly implausible levels of conservation risk. If anything, testing failed to fully explore scenarios where stock productivity was plausibly high. In this case, the simulation trials failed to assign sufficient priority to hunting need satisfaction.

Acknowledgments

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References


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Table 1: Abundance estimates and CVs. The CVs are approximations for the standard errors of log abundances.

<table>
<thead>
<tr>
<th>Year</th>
<th>Estimate</th>
<th>CV</th>
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<tbody>
<tr>
<td>1978</td>
<td>4765</td>
<td>0.305</td>
</tr>
<tr>
<td>1980</td>
<td>3885</td>
<td>0.343</td>
</tr>
<tr>
<td>1981</td>
<td>4467</td>
<td>0.273</td>
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<tr>
<td>1982</td>
<td>7395</td>
<td>0.281</td>
</tr>
<tr>
<td>1983</td>
<td>6573</td>
<td>0.345</td>
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<tr>
<td>1985</td>
<td>5762</td>
<td>0.253</td>
</tr>
<tr>
<td>1986</td>
<td>8917</td>
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<td>1987</td>
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<td>1988</td>
<td>6928</td>
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<td>1993</td>
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<tr>
<td>2001</td>
<td>10545</td>
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<tr>
<td>2008</td>
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<tr>
<td>2011</td>
<td>16892</td>
<td>0.058</td>
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Table 2: Lower triangular portion of the correlation matrix for log abundances.

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<tr>
<th>Year</th>
<th>Correlation matrix</th>
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<td>0.118 1.000</td>
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<td>1981</td>
<td>0.056 0.50 1.000</td>
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<td>1982</td>
<td>0.094 0.084 0.035 1.000</td>
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<td>1985</td>
<td>0.070 0.062 0.020 0.078 0.062 1.000</td>
</tr>
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<td>1986</td>
<td>0.072 0.064 0.017 0.092 0.064 0.113 1.000</td>
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<td>1987</td>
<td>0.124 0.110 0.052 0.088 0.110 0.065 0.067 1.000</td>
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<td>2011</td>
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Table 3: Estimates of parameters obtained from the overall fit and 13 cross-validation fits. The first column indexes the deleted survey in time order, with “0” representing the full fit. Some of the estimates of $K$ exceeded our imposed bound of 1,000,000; these entries are denoted ‘unbd’.

<table>
<thead>
<tr>
<th>$i$</th>
<th>$P_{1914}$</th>
<th>$s_0$</th>
<th>$s$</th>
<th>$m$</th>
<th>$p$</th>
<th>$f_{\text{max}}$</th>
<th>$\lambda_{\text{max}}$</th>
<th>$K$</th>
<th>MSYR</th>
<th>MSYL</th>
<th>$z$</th>
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<tbody>
<tr>
<td>0</td>
<td>1,114</td>
<td>0.976</td>
<td>0.979</td>
<td>30</td>
<td>23</td>
<td>0.583</td>
<td>1.050</td>
<td>unbd</td>
<td>0.048</td>
<td>0.074</td>
<td>0.621</td>
</tr>
<tr>
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<td>729</td>
<td>0.974</td>
<td>0.988</td>
<td>30</td>
<td>25</td>
<td>0.569</td>
<td>1.055</td>
<td>103,972</td>
<td>0.055</td>
<td>0.140</td>
<td>1.521</td>
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<td>0.984</td>
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<td>0.052</td>
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<td>0.986</td>
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<td>24</td>
<td>0.536</td>
<td>1.050</td>
<td>139,507</td>
<td>0.050</td>
<td>0.142</td>
<td>1.360</td>
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<td>0.990</td>
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<tr>
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<td>0.986</td>
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<td>26</td>
<td>0.605</td>
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<td>0.244</td>
<td>1.661</td>
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<td>0.985</td>
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<td>0.580</td>
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<td>0.053</td>
<td>0.111</td>
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<td>294,178</td>
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<td>0.121</td>
<td>1.575</td>
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<tr>
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<td>1.052</td>
<td>207,515</td>
<td>0.045</td>
<td>0.306</td>
<td>1.677</td>
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<td>0.978</td>
<td>0.981</td>
<td>30</td>
<td>25</td>
<td>0.550</td>
<td>1.051</td>
<td>108,369</td>
<td>0.043</td>
<td>0.219</td>
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</table>

Table 4: Point estimates and approximate 95% confidence intervals for model parameters. The parameters with asterisks have estimated confidence intervals produced by the simulation method described in the text. No confidence interval is given for MSYL; see the text.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>Lower</th>
<th>Upper</th>
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</thead>
<tbody>
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<td>1.212</td>
</tr>
<tr>
<td>$s_0$</td>
<td>0.976</td>
<td>0.974</td>
<td>0.979</td>
</tr>
<tr>
<td>$s_0$</td>
<td>0.979</td>
<td>0.974</td>
<td>0.981</td>
</tr>
<tr>
<td>$m^*$</td>
<td>30</td>
<td>24</td>
<td>30</td>
</tr>
<tr>
<td>$p$</td>
<td>23</td>
<td>23</td>
<td>25</td>
</tr>
<tr>
<td>$f_{\text{max}}$</td>
<td>0.583</td>
<td>0.581</td>
<td>0.616</td>
</tr>
<tr>
<td>$\lambda_{\text{max}}$</td>
<td>1.050</td>
<td>1.000</td>
<td>1.057</td>
</tr>
<tr>
<td>$K$</td>
<td>unbd</td>
<td>47,434</td>
<td>unbd</td>
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<tr>
<td>MSYR*</td>
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<td>0.033</td>
<td>0.056</td>
</tr>
<tr>
<td>$z^*$</td>
<td>0.621</td>
<td>0.000</td>
<td>3.220</td>
</tr>
</tbody>
</table>
Figure 1: Value of the negative log likelihood as a function of $S_0$ while holding the other parameters fixed at their MLEs. The horizontal lines correspond to the minimum value of the negative log likelihood and the deviance limit above it (see text). The vertical line indicates the MLE for $S_0$. 
Figure 2: Population trajectory from maximum likelihood estimates (red) and cross-validated fits. The dots and dashed lines show the point estimates and 95% confidence intervals for the time series of abundance estimates.