Surplus Production Modeling of Scaup Population Dynamics

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Abstract

Given the persistence of low scaup population levels, there continues to be interest in a decision-making framework for harvest management that acknowledges the limitation of extant monitoring programs and our incomplete understanding of population dynamics. We evaluated the potential of using a simple, surplus production (i.e., logistic growth) model to represent scaup population dynamics, coupled with a Bayesian estimation framework. We ultimately explored three different parameterizations of the surplus production model in which the intrinsic growth rate and carrying capacity were either constant or allowed to vary over time. We used stochastic dynamic programming to investigate the harvest-management implications of each model. Overall, each model provided a good approximation of observed scaup population and harvest dynamics. Model-based harvest-rate estimates suggest that scaup harvest rates have increased since the inception of the Adaptive Harvest Management program, while breeding populations have continued to decline. We observed distinct differences in the optimal harvest policies under each model. Caution should be exercised in applying these results to harvest management, however, because there are as yet unresolved issues associated with model specification and selection, as well as with the biological interpretation of the fitted models. Despite these issues, we believe our modeling framework provided an efficient representation of scaup population dynamics, balancing the trade-off between model complexity and the limited monitoring information available for scaup. Moreover, the Bayesian estimation framework provides parameter estimates and predictions in the form of probability distributions that are useful for informed decision making under uncertainty. While we believe it is too early to consider regulatory changes for scaup, additional analyses and exploration are warranted. Future work will focus on evaluating the implications of using different functional forms of the surplus production model as well as investigating methods for model selection.
Introduction

The ability to make informed decisions to regulate scaup (greater *Aythya marila* and lesser *Aythya affinis*) harvest levels is constrained by the limited amount of biological information describing scaup population dynamics and an incomplete understanding of how scaup populations respond to harvest management. The continued persistence of low scaup populations relative to the North American Waterfowl Management Plan (NAWMP) goal has resulted in concerns among managers that question how the current harvest regulations may be affecting scaup populations. Moreover, these concerns have highlighted a need to develop a more rigorous decision-making framework for scaup harvest management that is model-based, providing a structure for prediction and simulation while realistically representing the uncertainty that characterizes our ability to monitor scaup populations and our understanding of scaup population dynamics.

A traditional balance equation (i.e., the decomposition of cohort-specific growth processes) cannot be used to model scaup population dynamics because of the limited amount of available demographic information describing scaup populations. However, alternative modeling approaches exist that can be used to represent an exploited population without sex and age-specific survival and harvest rates. For example, surplus or biomass production models are often used in fisheries stock assessments because they can represent changes in overall stock biomass from limited survey, catch, and effort information while still providing useful information for decision making in the form of management parameters (Hilborn and Walters 1992, Quinn and Deriso 1999). With this formulation, population dynamics can be modeled with a simple difference equation that relates total population size (pooled over sex and age classes) in a current year to last year’s population plus net recruitment less losses from the harvest. As a result, the detailed survival and recruitment dynamics represented with the traditional balance equation are simplified into a few parameters that describe how the overall population changes from year to year and responds to exploitation. Fisheries scientists have also developed estimation frameworks that can be used to derive parameter and population estimates for formal stock assessments which may be useful for decision making in harvest management (Quinn and Deriso 1999).

Given the existing monitoring information available for scaup, we evaluated the potential of using a simple, surplus production modeling approach to assess scaup population dynamics and as a population modeling framework useful for informed decision making. It is anticipated that this assessment work will provide parameter estimates useful for management in addition to realistic representations of the sources of uncertainty that could be used to evaluate management implications in a more rigorous decision-making framework.

Methods

For this initial assessment, we focused on the existing time series of information that describes scaup population dynamics. These data include spring breeding population estimates from the traditional survey area from 1961 - 2002, harvest estimates from the U.S. (1961 – 2002) and Canada (1974 – 2002), and estimates of hunting effort (total hunter days) in the U.S. from 1961 - 2002. All numbers were taken from the recent review of scaup status (Allen et al. 1999) and

**Surplus Production Model**

We modeled scaup population dynamics within a surplus production modeling framework (Hilborn and Walters 1992, Quinn and Deriso 1999). With this approach, we used a logistic, difference equation to model changes in population size $N$ in year $t$ according to

$$N_{t+1} = N_t + rN_t(1 - \frac{N_t}{K}) - H_t,$$

where $r$ is the intrinsic rate of population growth, $K$ is the carrying capacity, and $H$ is the total harvest in year $t$. In the logistic model we note that, strictly speaking, harvest is an additive form of mortality. However, it is important to recognize that compensatory responses in both the survival and reproductive processes occur as a response to harvest-related reductions in breeding population size. With this very simple model, population change is governed by two population parameters, but more importantly, it couples the harvest process with changes in population size. This is the fundamental connection that will enable us to cast a population model into a decision-making framework that explicitly relates population predictions (model-based) as a function of policy decisions in a harvest management context.

**Assessment Framework**

The goal of this assessment work is to develop a framework to represent scaup population dynamics with an ability to predict changes in population sizes with annually-updated monitoring information. In order for these predictions to be useful in a management context, decision makers must be able to make probabilistic statements regarding the likelihood of a particular outcome. Therefore, the model requires parameter estimates and realistic representations of their variances. Ideally, an assessment model must be able to not only represent the uncertainty associated with the monitoring information (observation error) but must also include structure to account for uncertainty associated with variation in population change (process error). Therefore, we used an existing Bayesian estimation framework (Meyer and Millar 1999, Millar and Meyer 2000) originally developed for fisheries management that explicitly considers both of these types of uncertainty to estimate the scaup population parameters while also providing probability distributions associated with population predictions.

**Process Model**

We used a state space representation of the Schaefer (1954) surplus production model developed by Meyer and Millar (1999) and Millar and Meyer (2000). With this parameterization, the deterministic equation (1) representing population change is recast into a stochastic population model with population numbers expressed as a proportion of the carrying capacity (i.e., $P_t = \frac{N_t}{K}$)
\[ P_t = e^{\varepsilon_t} \]  
\[ P_{t+1} = (P_t + rP_t(1 - P_t) - H_t / K)e^{\varepsilon_t}, t = 2, ..., T \]  

and,

\[ \varepsilon_t \sim N(0, \sigma^2_{\text{Process}}). \]  

This formulation then explicitly acknowledges our incomplete understanding of the variability associated with how scaup populations change from year to year.

We included additional structure in the population model by separating out the harvest from the U.S. and Canada with

\[ H_t = H_{\text{USA}}^t + H_{\text{Can}}^t, \]  

where \( H_{\text{USA}}^t \) and \( H_{\text{Can}}^t \) represent the harvest recorded in the U.S. and Canada respectively. In order to provide a functional connection between changes in hunter effort (total duck days) and the harvest, we modeled the U.S. harvest process as a function of the hunter effort data

\[ H_{\text{USA}}^t = h_{\text{USA}}^t P_t K \]  
\[ h_{\text{USA}}^t = q E_{\text{USA}}^t \]

where \( h_{\text{USA}}^t \) is the crude harvest rate in the U.S. in year \( t \) and \( q \) is a catchability term that represents the expected harvest rate given one unit of effort (\( E_{\text{USA}}^t \)) observed in the U.S. in year \( t \).

**Observation Model**

We used the data described above to relate the unknown population and harvest numbers represented in the model (\( P_t \) and \( H_{\text{USA}}^t \)) with the observed population and harvest numbers (US) collected by the monitoring program (\( \hat{N}_t \) and \( \hat{H}_{\text{USA}}^t \)). We assumed that the observation process yielded, additive, normally distributed errors which we represented with

\[ N_t = P_t K + \varepsilon_{t, \text{BPOP}} \]  
\[ H_{\text{USA}}^t = P_t K q E_{\text{USA}}^t + \varepsilon_{t, \text{Harvest}} \]  
\[ \varepsilon_{t, \text{BPOP}} \sim N(0, \sigma^2_{\text{BPOP}}), \text{and} \]  
\[ \varepsilon_{t, \text{Harvest}} \sim N(0, \sigma^2_{\text{Harvest}}). \]  

\[ \varepsilon_{t} \sim N(0, \sigma^2_{\text{Process}}). \]
It is important to note that we were able to incorporate estimates of $\sigma_{BPOP}^2$ for each year from the breeding population monitoring program. We did not have estimates of the sampling errors associated with the harvest data survey $\sigma_{Harvest}^2$, therefore we used a vague prior to represent this variation.

**Bayesian Estimation**

From a Bayesian analysis and decision-making perspective, we are interested in making probabilistic statements about model parameters conditional on the information observed in the data (Gelman et al. 1995). That is, we are interested in evaluating $P(\theta | data)$ which requires the specification of prior distributions for all model parameters and the unobserved system states $P(\theta)$ and the sampling distributions (likelihood) for the observed data $P(data | \theta)$. Using Bayes theorem, we can then represent the posterior distribution $P(\theta | data)$, with

$$P(\theta | data) \propto P(\theta) \times P(data | \theta).$$

Following Meyer and Millar (1999) we developed a fully conditional joint probability model, by first proposing prior distributions for all model parameters and unobserved system states and secondly by developing a fully conditional likelihood for each sampling distribution.

**Priors**

For this analysis, a joint prior distribution is required because the unknown system states $P$ are assumed to be conditionally independent (Meyer and Millar 1999). This leads to the following joint prior distribution for the model parameters and unobserved system states

$$P(r, K, q, \sigma_{process}^2, \sigma_{Harvest}^2, P_{1,...,n})$$

$$= p(K) p(q) p(\sigma_{process}^2) p(\sigma_{Harvest}^2) p(P_1 | \sigma_{process}^2) \times \prod_{i=2}^{n} p(P_i | P_{i-1}, r, K, q, \sigma_{process}^2)$$

(12)

We chose vague priors for $r$ and $K$ with parameterizations specified within biological bounds, while non informative priors were specified for $q$, $\sigma_{process}^2$ and $\sigma_{Harvest}^2$ as follows:

- $K \sim$ Lognormal (2.17, 1.50)
- $r \sim$ Lognormal (0.25, 0.25)
- $q \sim$ Inverse-gamma (0.001, 0.001)
- $\sigma_{process}^2 \sim$ Inverse-gamma (0.001, 0.001)
- $\sigma_{Harvest}^2 \sim$ Inverse-gamma (0.001, 0.001).
**Likelihood**

We related the observed population and US harvest estimates to the model parameters and unobserved system states with the following likelihood function:

\[
P(N_{1\ldots T}, H_{1\ldots T}^{USA} | K, q, \sigma^2_{process}, \sigma^2_{Harvest}, P_{1\ldots T})
\]
\[
= \prod_{t=1}^{T} p(N_t | P_t, K, \sigma^2_{BPOP}) \times \prod_{t=1}^{T} p(H_t^{USA} | P_t, K, q, E_t, \sigma^2_{Harvest}).
\]

(13)

**Posterior Evaluation**

Using Bayes theorem we then specified a posterior distribution for the fully conditional joint probability distribution of the parameters given the observed information

\[
P(r, K, q, \sigma^2_{process}, \sigma^2_{Harvest}, P_{1\ldots T} | N_{1\ldots T}, H_{1\ldots T}^{USA})
\]
\[
= p(K) p(q) p(\sigma^2_{process}) p(\sigma^2_{Harvest}) p(P_1 | \sigma^2_{process}) \times \prod_{t=2}^{T} p(P_t | P_{t-1}, E_t, r, K, q, \sigma^2_{process}) \times \prod_{t=1}^{T} p(N_t | P_t, K, \sigma^2_{BPOP}) \times \prod_{t=1}^{T} p(H_t^{USA} | P_t, K, q, E_t, \sigma^2_{Harvest}).
\]

(14)

We used Markov Chain Monte Carlo (MCMC) methods to evaluate this posterior distribution using WinBUGS (Spiegelhalter et al. 2003). After an initial burn-in period of 50,000 iterations, an additional 200,000 iterations of a chain were run; this chain was then thinned by 25, yielding a sample of 8000 points. Additional runs with multiple chains were simulated and Gelman-Rubin statistics (Brooks and Gelman 1998) were calculated for all nodes. These results indicated that the Markov chain had converged. In addition to checking convergence, these additional runs were also used to test simulation results with different initial parameter values that were randomly generated from uniform distributions. During this testing, we recorded several instances where the sampler in WinBUGS failed. These situations were resolved by changing the bounds of the uniform distribution.

**Candidate Model Set**

The continued persistence of scaup population levels less than the NAWMP goal suggests that the inherent dynamics of this population have changed over time, possibly in response to large-scale system changes (Austin et al. 2000). In order to allow for these changes in our population model, this system change may be represented as a change in the intrinsic rate of increase \(r\), the carrying capacity \(K\), or some other latent factor that is not included our current formulation. We explored parameterizations that allowed population parameters to change over time by letting \(r\) or \(K\) vary each year according to a simple random walk similar to a formulation presented by Fournier (2001):
\[ r_t = r_{t-1}e^{\epsilon_{t}} \]
\[ K_t = K_{t-1}e^{\epsilon_{t}} \]

where,
\[ \epsilon_{t} \sim N(0, \sigma_{Walk}^2) \]

Based on this re-parameterization, we developed a candidate model set that represented explicit differences in how \( r \) or \( K \) was allowed to vary in the population assessment (Table 1). We then performed population assessments with each model to evaluate model performance and compare and contrast parameter estimates and population predictions. In addition, we predicted the 2003 breeding population size based on the population, harvest, and effort information observed in year 2002. Total duck days measured by the Harvest Information Program (HIP) in 2002 was translated into an effort measure comparable to the total duck days recorded by the historical Mail Questionnaire Survey (MQS) based on a regression equation derived from data from both surveys (1999-2001). Finally, we explored the management implications of using each model in an optimal decision-making framework.

Table 1. The candidate model set used to assess scaup populations within the Bayesian estimation framework.

<table>
<thead>
<tr>
<th>Model</th>
<th>( r )</th>
<th>( K )</th>
</tr>
</thead>
<tbody>
<tr>
<td>M0</td>
<td>Constant</td>
<td>Constant</td>
</tr>
<tr>
<td>M1</td>
<td>Varies according to a random walk</td>
<td>Constant</td>
</tr>
<tr>
<td>M2</td>
<td>Constant</td>
<td>Varies according to a random walk</td>
</tr>
</tbody>
</table>

Results

Model Fitting

The Bayesian population assessments using models M0, M1, and M2 provided satisfactory fits to the observed breeding population and harvest information with reasonable estimates of variation associated with the posterior mean of each estimate (Figures 1-3; A and B). Crude harvest rates calculated as a function of the catchability parameter \( (q) \) and the level of observed effort (total duck days) were variable ranging from 0.0376 to 0.105 and were very similar regardless of which model was used (Figures 1-3; C). In general, scaup harvest rates tracked population levels from the mid 1960’s until the early 1990’s. However, the results from this assessment suggest that this relationship may have changed starting in the early 1990’s when harvest rates increased while population sizes have continued to decline (Figure 1-3; D).

Estimates of population size, harvest levels, and harvest rates were all very similar regardless of which model was used in the assessment. However, the parameter estimates for \( r \) or \( K \) and the process variances \( (\sigma_{\text{process}}^2) \) were variable depending on which model was used in the assessment (Table 2). Interestingly, the catchability parameter estimates \( (q) \) and the harvest variance \( (\sigma_{\text{Harvest}}^2) \) were similar regardless of which model was used for the assessment. When \( r \) was
allowed to vary, the random walk resulted in an increase in the intrinsic rate of increase during the 1970’s with a peak or maximum value occurring in 1978 (Figure 4). This peak was then followed by a steady decline over the 1980’s resulting in a persistent minimum for the last 15 years. The changes associated with this random walk were variable resulting in wide credibility intervals. In contrast, the random walk for the carrying capacity was less variable and resulted in a pattern for $K$ that tracked changes in estimated population sizes, resulting in a distinct and persistent reduction in the value for $K$ as the population has continued to decline (Figure 5). Population predictions calculated for year 2003 with parameter estimates from the population assessments based on model M0 (3.774), M1 (3.510), and M2 (3.700), were very similar to the observed breeding population size equaling 3.734 million birds (see Table 2).
Figure 1. Population assessment results based on a Bayesian analysis using model M0 and scaup population and harvest data from 1961-2002. A. The posterior mean population sizes and 95% credibility intervals plotted with the observed breeding population estimates. B. The posterior mean harvest and 95% credibility intervals plotted with the observed harvest levels resulting from the harvest survey program. C. Crude harvest rates (posterior means) and 95% credibility intervals calculated as a function of catchability ($q$) and the level of effort (total duck days) measured each year. D. The posterior mean scaup population levels and estimated harvest rates (posterior means) resulting from model M0.
Figure 2. Population assessment results based on a Bayesian analysis using model M1 and scaup population and harvest data from 1961-2002. A. The posterior mean population sizes and 95% credibility intervals plotted with the observed breeding population estimates. B. The posterior mean harvest and 95% credibility intervals plotted with the observed harvest levels resulting from the harvest survey program. C. Crude harvest rates (posterior means) and 95% credibility intervals calculated as a function of catchability ($q$) and the level of effort (total duck days) measured each year. D. The posterior mean scaup population levels and estimated harvest rates (posterior means) resulting from model M1.
Figure 3. Population assessment results based on a Bayesian analysis using model M2 and scaup population and harvest data from 1961-2002. A. The posterior mean population sizes and 95% credibility intervals plotted with the observed breeding population estimates. B. The posterior mean harvest and 95% credibility intervals plotted with the observed harvest levels resulting from the harvest survey program. C. Crude harvest rates (posterior means) and 95% credibility intervals calculated as a function of catchability ($q$) and the level of effort (total duck days) measured each year. D. The posterior mean scaup population levels and estimated harvest rates (posterior means) resulting from model M2.
Table 2. Parameter estimates (posterior means) and 95% credibility intervals (LCI, UCI) resulting from the Bayesian analysis based on models M0, M1, and M2, using scaup population and harvest data from 1961-2003.

<table>
<thead>
<tr>
<th>$\theta$</th>
<th>Model M0</th>
<th></th>
<th></th>
<th></th>
<th>Model M1</th>
<th></th>
<th></th>
<th></th>
<th>Model M2</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>LCI</td>
<td>UCI</td>
<td>Mean</td>
<td>LCI</td>
<td>UCI</td>
<td>Mean</td>
<td>LCI</td>
<td>UCI</td>
<td>Mean</td>
<td>LCI</td>
<td>UCI</td>
</tr>
<tr>
<td>$r$</td>
<td>0.2990</td>
<td>0.1509</td>
<td>0.4845</td>
<td>0.1737$^a$</td>
<td>0.0007</td>
<td>0.6183</td>
<td>1.0100</td>
<td>0.3339</td>
<td>1.7670</td>
<td></td>
<td></td>
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<tr>
<td>$q$</td>
<td>0.0062</td>
<td>0.0054</td>
<td>0.0069</td>
<td>0.0063</td>
<td>0.0055</td>
<td>0.0070</td>
<td>0.0063</td>
<td>0.0056</td>
<td>0.0071</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\sigma^2_{process}$</td>
<td>0.0150</td>
<td>0.0080</td>
<td>0.0265</td>
<td>0.0078</td>
<td>0.0018</td>
<td>0.0193</td>
<td>0.0024</td>
<td>0.0004</td>
<td>0.0076</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\sigma^2_{Harvest}$</td>
<td>0.0249</td>
<td>0.0156</td>
<td>0.0393</td>
<td>0.0242</td>
<td>0.0153</td>
<td>0.0378</td>
<td>0.0246</td>
<td>0.0156</td>
<td>0.0381</td>
<td></td>
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<tr>
<td>$\sigma^2_{Walk}$</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
<td>0.4866</td>
<td>0.0417</td>
<td>2.0810</td>
<td>0.0052</td>
<td>0.0018</td>
<td>0.0116</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^a$ Parameter values listed for models M1 and M2 that were modeled with a random walk refer to the 2002 estimates.

$^b$ The 2003 breeding population predictions in millions of birds were based on the population and harvest information from 2002 (see text).
Figure 4. The random walk (posterior means) and corresponding 95% credibility intervals of the intrinsic rate of increase (r) resulting from the Bayesian population assessment using model M1 and scaup population and harvest data from 1961 - 2002.
Figure 5. The random walk (posterior means) and 95% credibility interval of the carrying capacity term ($K$) resulting from the Bayesian population assessment using model M2 and scaup population and harvest data from 1961 - 2002.
Management Implications

In this section we provide some implications of the three scaup population models for harvest management. In the theory of maximum sustained yield (MSY), parameters of interest in harvest management can be derived directly from the logistic model of population growth. The standard logistic model describes a parabolic relationship between equilibrium population sizes \(N\) and sustainable harvests \(H\), such that the maximum harvest is attained at a population size one-half of the carrying capacity \(K\) (Figure 6). The harvest rate \(h\), expressed as \(H/N\) attendant to this maximum harvest is one-half the rate of growth \(r\) and the maximum harvest is \(rK/4\).

A major shortcoming in classic MSY theory, however, is the failure to account for uncontrolled environmental factors that prevent populations from achieving equilibrium. It has been known for almost three decades that managing for a constant level of harvest in a randomly fluctuating environment can lead to irreversible population declines (Beddington and May 1977, Larkin 1977). Moreover, classic MSY theory neither accounts for potential temporal changes in \(r\) or \(K\), nor for the limitations of the logistic model to describe observed changes in population size. We overcame these shortcomings by using discrete, stochastic dynamic programming (Puterman 1994) to derive a closed-loop harvest strategy for each of the three scaup population models. Closed-loop harvest strategies involve a feedback mechanism whereby harvests are adjusted periodically based on observed rather than predicted population size.

We used generalized software developed by Lubow (1995) to derive model-specific harvest strategies intended to maximize the long-term cumulative sum of undiscounted, annual harvests. Many other management objectives are possible, but we believed an objective to maximize long-term cumulative harvest would serve as a useful reference point. For each model we evaluated harvest levels (U.S. and Canada combined) of 0-4 million (in increments of 25 thousand), for population sizes of 0-7 million (in increments of 250 thousand). We assumed perfect controllability of harvests throughout. For Models M1 and M2, respectively, we calculated optimal harvests for values of \(r\) of 0.1-1.5 (in increments of 0.1) and for values of \(K\) of 2-7 million (in increments of 0.5 million). In each case we accounted for model-specific process errors, which specify the degree to which a particular model failed to perfectly describe scaup population dynamics. Process errors were assumed to be distributed normally with mean = 0 and variance equal to its posterior mean. We discretized the distributions of process error by using the 10\(^{th}\), 30\(^{th}\), 50\(^{th}\), 70\(^{th}\), and 90\(^{th}\) quantiles as support points and assigning them each a probability mass of 20 percent. We treated the distributions of the random walks for \(r\) and \(K\) in the same fashion. Finally, we found it necessary to impose bounds on the temporal variation of \(r\) in order to derive a stationary strategy (i.e., one in which optimal harvests are dependent on population size but not on time). We used bounds of 0.5-2.0 based on inspection of posterior distributions of \(r\) under Model 1.

Model-specific optimal harvest strategies are depicted graphically in Figures (7-9). The optimal harvest strategy associated with Model 0 prescribes zero harvests for \(N < 2.75\) million (see Figure 7). The optimal level of harvest then increases sharply with increases in \(N\). As \(N\) reaches \(K = 6.837\) million the optimal harvest is that required to return the population to \(K/2\).
For Model 1, optimal harvest levels increase with both increases in $N$ and $r$, although the effect of $N$ is much more pronounced (see Figure 8). In contrast to Model 0, non-zero harvests are permitted for $N < 2.5$ million if $r$ is sufficiently high. For very high levels of $r$, the optimal harvest level approaches 4 million for population sizes of 5-6 million, but then declines as $N$ approaches and then exceeds the carrying capacity of $K = 6.577$ million. This behavior of the harvest strategy is due to the strong negative feedback induced by a high $r$, such that populations above carrying capacity will decline sharply even in the absence of harvest.

The optimal harvest strategy associated with Model 2 appears relatively liberal for most population sizes, in large part due to the high estimate of $r = 1.01$ (see Figure 9). As in Model 1, optimal levels of harvest increase with $N$ but then decline as populations exceed $K$. This optimal strategy also exhibits some pathological behavior associated with Model 2. When $N$ is very high relative to $K$, the model predicts an immediate population extinction. Therefore, the optimal strategy is to harvest the entire population (or the maximum admissible amount; 4 million in this case) because there will be no harvests available in subsequent years. This phenomenon can be seen in the lower right corner of Figure 9. This pathological behavior is exhibited by the discrete logistic model whenever $r < rN/K - 1$, and clearly is biologically unrealistic. Fortunately, we would rarely expect to encounter this condition in nature.

We next compared observed levels of harvest during 1998-2002 with model-specific optima (Table 3). In most cases, observed harvest was similar to or significantly less than the optimum.
Figure 6. Equilibrium population sizes and associated sustainable harvests (in millions) from a discrete, deterministic logistic model in which $r = 0.299$ and $K = 6.837$ million. The vertical dashed line represents $N = K/2$, which is the equilibrium population size that maximizes sustainable harvest.
Figure 7. Optimal scaup harvest (H, in millions) as a function of observed population size (N, in millions) under Model 0, in which the intrinsic rate of growth $r = 0.299$ and carrying capacity $K = 6.837$ million.
Figure 8. Optimal scaup harvest (contours, in millions) as a function of observed population size (N, in millions) and intrinsic growth rate (r) under Model 1, in which carrying capacity $K = 6.577$ million.
Figure 9. Optimal scaup harvest (contours, in millions) as a function of observed population size (N, in millions) and carrying capacity (K, in millions) under Model 2, in which the intrinsic rate of growth $r = 1.01$. 
Table 3. Observed scaup population sizes ($N$, in millions) and harvests ($H$, U.S. and Canada combined, in millions) for 1998-2002 compared with approximate optimal harvests ($H^*$, in millions) under each population model. Under Models 1 and 2, $r$ and $K$ represent the estimates of intrinsic growth rate and carrying capacity (in millions), respectively.

<table>
<thead>
<tr>
<th>Year</th>
<th>$N$</th>
<th>$H$</th>
<th>$H^*$</th>
<th>$r$</th>
<th>$H^*$</th>
<th>$K$</th>
<th>$H^*$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>3.472</td>
<td>0.667</td>
<td>0.500</td>
<td>0.23</td>
<td>0.472</td>
<td>4.43</td>
<td>2.075</td>
</tr>
<tr>
<td>1999</td>
<td>4.412</td>
<td>0.300</td>
<td>1.525</td>
<td>0.17</td>
<td>1.305</td>
<td>4.68</td>
<td>2.225</td>
</tr>
<tr>
<td>2000</td>
<td>4.026</td>
<td>0.434</td>
<td>1.025</td>
<td>0.14</td>
<td>0.885</td>
<td>4.56</td>
<td>2.225</td>
</tr>
<tr>
<td>2001</td>
<td>3.694</td>
<td>0.438</td>
<td>0.775</td>
<td>0.14</td>
<td>0.495</td>
<td>4.34</td>
<td>2.100</td>
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<tr>
<td>2002</td>
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<td>0.508</td>
<td>0.500</td>
<td>0.17</td>
<td>0.472</td>
<td>4.23</td>
<td>1.975</td>
</tr>
</tbody>
</table>

Discussion

The Bayesian population assessment based on the discrete form of the Schaefer (1954) surplus production model resulted in a reasonable representation of population change based on a limited amount of information. The state space formulation of Meyer and Millar (1999) provided an efficient estimation framework that realistically accounted for process and observation uncertainty. From a decision-making context, the results of the Bayesian assessment are useful because of the probability distributions associated with each estimate permits one to make probabilistic statements regarding population predictions as well as characterize the uncertainty surrounding the population parameter and derived management parameter estimates.

Despite the utility of the analyses presented in this report, we suggest that considerable caution is warranted in using the models in this report for harvest-management purposes. First, application of the fitted models requires that we impart biological meaning to model parameters $r$ and $K$ (i.e., they accurately describe the mechanisms underlying changes in population size). However, the interpretation of these parameters is ambiguous, despite the satisfactory fit of the three models to available population and harvest data. This ambiguity arises because of the retrospective (i.e., correlative) nature of the analysis. Secondly, we only considered a single functional form of the logistic model. This functional form describes a perfectly symmetric growth curve with an inflection point (i.e., the population size with the highest harvestable surplus) at $K/2$. Non-symmetric growth curves are possible and may be the norm in nature. Fowler (1981) hypothesized that $K$-selected species may experience the greatest density-dependent effects on growth rate at populations sizes only slightly less than $K$. If this were true for scaup, we would expect the harvest strategies to be much more conservative than those described in this report. We thus consider the investigation of different functional forms of the logistic model to be a high priority in duck harvest management. Finally, we are disturbed by the ethical or social implications of Model 2. Under this model, if $K$ were declining due to uncontrollable changes in the environment, harvest managers would continue to drive the population to $K/2$. This may be the path to maximizing the long-term cumulative harvest, but it implicitly ignores other objectives that are likely to take precedence as a population experiences a long-term decline.
Despite these limitations, the results of this initial assessment suggest that scaup harvest rates have increased since the inception of the Adaptive Harvest Management (AHM) program, while breeding population estimates have continued to decline. While we believe it is too early to consider regulatory changes, we believe that additional analyses and exploration are warranted. More specifically, we feel these results highlight the importance of developing a long-term harvest management policy for scaup that balances the trade-off between population recovery and harvest opportunity. To develop such a policy, issues of model selection, management objectives, and ultimately the coupling of regulatory actions with observable harvest responses will have to be addressed. The existing scaup assessment provides a useful first step in the development of a rigorous decision-making framework for a rational, long-term scaup harvest policy.

The population assessment results described above suggest that each of the models that were considered can provide population and management parameters useful for decision making. However, the results from the optimal decision analysis highlight the distinct implications of using each model. Ultimately, a credible model set must be identified for use in scaup harvest management. Therefore, we are concentrating our efforts on research designed to provide additional information useful for model selection. We are currently investigating the use of Deviance Information Criteria (DIC) as a metric to rank each model (Spiegelhalter et al. 2002) in addition to performing cross-validation experiments (Gelman et al. 2000). Additional work will continue to focus on issues of functional form and exploring different parameterizations to represent change in the logistic model.

**Literature Cited**


