

# Population viability analysis based on combining Bayesian, integrated, and hierarchical analyses

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## Abstract

Several methods used in fisheries stock assessment models that can be applied to population viability analysis are presented. (1) Integrated analysis allows the use of all information on a particular population, and ensures that all model assumptions and parameter are consistent throughout the analysis, that uncertainty is propagated throughout the analysis, and that the correlation among parameters is preserved. (2) Bayesian analysis allows for the inclusion of prior information, and is a convenient way to represent uncertainty. (3) Random-effects models based on hierarchical modeling allow information to be shared among parameter estimates and allow the separation of process error from estimation error. (4) Non-parametric representation of parameters allows for a more flexible relationship among the parameters. (5) Robust likelihood functions provide an automatic method to reduce the influence of outliers when the data sets are large. These methods are applied to artificial data sets provided by the Extinction Risk Working Group of the National Center for Ecological Analysis and Synthesis (NCEAS) using AD Model Builder software (Otter Research™).

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## 1. Introduction

Population viability analysis (PVA) is a tool commonly used in conservation biology to evaluate the risk of extinction and to evaluate management strategies. In general, PVA uses a population dynamics model and estimates of the model parameters to project the population forward in time. Typically, demographic stochasticity is added to the model to provide an indication of the future uncertainty. This requires projecting the model forward in time multiple times with the demographic parameters randomly selected from appropriate distributions. Demographic stochasticity is only one component of the total uncertainty and is often less than the other components, which include parameter and model structure uncertainty. Parameter uncertainty is usually included by representing parameters with distributions rather than point estimates. These distributions are usually taken from independent analyses (e.g. mark-recapture studies). Model structure uncertainty is seldom included in PVA, and is usually used only as a sensitivity analysis.

PVAs, in the form outlined above, usually do not use all available information. Some ignore dependencies. There may be additional information about the parameters of the PVA model in the data used in the independent analyses that is not available to the PVA, and other types of data (e.g. abundance trend) are not included in the analysis. It is not common practice to fit conservation biology models to multiple data types. The assumption that parameters are independent may produce greater levels of uncertainty and unrealistic model predictions. For example, low biomass and high survival or high biomass and low survival may produce realistic abundance trends, but not high biomass and high survival or low biomass and low survival. Fitting the model to abundance trend information would allow the estimation of this correlation.

Fisheries stock assessment modeling has been based on the need to provide advice in an environment lacking in data (this is less true for some areas, including Europe and the east coast of the United States and Canada, that have a long histories of collecting catch-at-age information). Therefore, fisheries modelers have strived to include information from wherever possible and to represent the uncertainty in model

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estimates. This has led to the development of several methods that add information to the analysis: (1) integrating multiple data types; (2) sharing information among populations or species (meta analysis); (3) sharing information among parameters that differ by time or another factor (hierarchical models, random-effects, random walks, and smoothing penalties); (4) prior information (Bayesian analysis); and including scientific understanding (structural models and functional forms). The complex models used in fisheries require statistical estimation methods that are efficient and robust to data contamination.

In 2002 the Extinction Risk Working Group of the National Center for Ecological Analysis and Synthesis (NCEAS) held a competition to predict the probability of extinction and population decline for several artificial data sets (McCarthy et al., *in press*). The competition was designed to determine how well models could predict the probability of extinction and population decline, and how these predictions compared to subjective estimates. The numbers of individuals of each of four hypothetical populations (a frog, snail, small mammal, and small plant) were projected over time, and artificial data sets were created. In addition to the data, a brief description of each population, including notes on its biology, was provided. The characteristics used to represent the populations included prey, cannibalism, inbreeding, and dynamics in response to weather. The data included line transects, quadrat surveys, and total counts. Some of the data sets were stratified by age, stage, and/or sex. Not all the population characteristics or data were included for each population. For a full description of the populations, see McCarthy et al. (*in press*).

I applied recent developments in fisheries stock assessment modeling to these data sets to determine how well they would work on non-fish species, particularly species for which I have little prior knowledge. On average, these analyses performed better than most of the quantitative analyses and subjective judgments submitted to the competition that were carried out by researchers working in the field of extinction risk for terrestrial species and the predictions were of comparable quality to those that were closest to the truth (Fig. 1; McCarthy et al., *in press*). The recent developments I applied included integrated analysis (e.g. Fournier and Archibald, 1982; Methot, 1990; Fournier et al., 1998; Maunder, 2001a,b), Bayesian analysis to represent uncertainty and include prior information (see the reviews in Punt and Hilborn, 1997; McAllister and Kirkwood, 1998; e.g. McAllister et al., 1994; McAllister and Ianelli, 1997; Maunder et al., 2000; Maunder and Starr, 2001), random-effects (hierarchical) modeling of process error (e.g. McAllister et al., 1994; Maunder and Watters, 2003), and non-parametric parameter representation (e.g. Fournier et al., 1998; Haist et al., 1999). The use of likelihood functions that are robust to outliers are important because of the large data sets used in these models (Fournier et al., 1990; Fournier et al., 1998). The models I applied to the artificial data sets were implemented with AD Model Builder (Otter Research™; see the review by Maun-

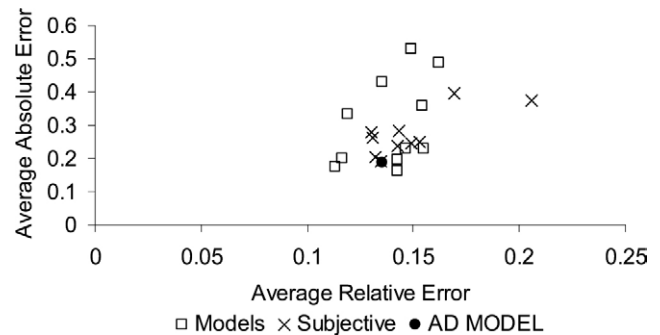


Fig. 1. Comparison of results from the methods presented in this paper (AD MODEL) applied to the data from the Extinction Risk Working Group of the National Center for Ecological Analysis and Synthesis (NCEAS) competition compared with other quantitative analysis and subjective judgment entries (data from McCarthy et al., *in press*).

der, 2000). In this document I describe these recent developments in fisheries stock assessment in relation to modeling endangered species and the prediction of the probability of extinction and population decline. Further details of these methods can be found in the relevant fisheries literature cited in the respective sections. Readers requiring a foundation in statistical model fitting and Bayesian analysis should refer to Hilborn and Mangel (1997).

## 2. Integrated analysis

The aim of integrated analysis is to include all data for a single population into one analysis. Traditionally, data are often analyzed in one analysis, and the summary statistics are used in a second analysis. For example, survival is estimated from mark-recapture data, and then used in a population dynamics model. Maunder (1998) suggested that the two-step procedure described above has several disadvantages, due to the fact that (1) information is often lost in the mark-recapture analysis, (2) assumptions in the mark-recapture analysis are often inconsistent with those of the population dynamics model, (3) uncertainty may not be adequately transferred from the mark-recapture analysis procedure into the fitting of the population dynamics model, and (4) the separation of the analyses may reduce the ability to diagnose any lack of fit. Maunder (1998, 2001a,b) and Maunder and Watters (2003) suggest that combining the analyses can overcome many of these problems. Integrated analysis ensures that model assumptions and parameter estimates are consistent throughout the analysis, that uncertainty is propagated throughout the analysis, and that the correlation between parameters is preserved (Maunder, 1998). Integrated analysis is based on non-linear model estimation, and therefore provides a flexible framework to develop the appropriate model for each individual application.

There have been several examples of integrated analysis applied in fisheries stock assessment. Fournier and Archibald (1982) developed methods to integrate multiple data types into a single analysis and Methot (1990) developed this into a

general stock assessment model. Fournier et al. (1998) integrated length-frequency analysis with a stock assessment model. Maunder (2001a) developed a general method to integrate the standardization of catch and effort data into stock assessment models. Fournier and Archibald (1982) integrated the estimation of the stock-recruitment relationship into a catch-at-age stock assessment model. Maunder and Watters (2003) developed a general method to integrate environmental indices into population dynamics models. Ishii (1979) integrated effort data into a mark-recapture model for which the dynamics were based on those used in population dynamics models. Richards (1991) integrated tagging data into a simple stock assessment model, and Maunder (1998, 2001b) integrated tagging data into a catch-at-age stock assessment model.

The general method used to integrate two analyses is to parameterize them in such a way that both have parameters in common, and then simultaneously estimate all the parameters with the values of the parameters in common shared between the two analyses. The objective functions of the two analyses are combined, and the estimation procedure optimizes this combined objective function.

Take an example with two types of data ( $data_1$  and  $data_2$ ), one for each analysis, two sets of parameters ( $\theta_1$  and  $\theta_2$ ) consisting of  $n$  parameters for the first analysis,  $m$  parameters for the second analysis, and  $p$  parameters that are common between the two analyses. Let  $\theta_1 = \{a, b, c, d\}$  and  $\theta_2 = \{c, d, e, f\}$  so  $\theta_1 \cap \theta_2 = \{c, d\}$  and the parameter set for the integrated model is  $\theta_1 = \theta_1 \cup \theta_2 = \{a, b, c, d, e, f\}$ . The likelihood for the integrated model is  $L(data_1, data_2 | \theta_1) = L(data_1 | \theta_1) L(data_2 | \theta_1)$ , and the parameters are estimated by  $\max_{\theta_1} [L(data_1, data_2 | \theta_1)]$   $\theta_1 \in \mathbb{R}^{n+m-p}$ .

To illustrate integrated analysis, I describe the integration of mark-recapture data into the population dynamics model. Take a population that has age-specific release and recapture data and the annual measurement of effort used to sample the population. In this example, the individuals examined for marks are assumed to die. The population dynamics are modeled as  $N_{t+1,a+1} = N_{t,a} \varphi_a - C_{t,a}$ , where  $N_{t,a}$  is the number of individuals of age  $a$  at time  $t$ ,  $\varphi_a$  is the survival rate of individuals of age  $a$ , and  $C_{t,a}$  is the number of individuals of age  $a$  examined for marks in time  $t$ . It is assumed that all individuals die after age  $A$  ( $\varphi_A = 0$ ). The parameters of the population dynamics model that must be estimated are the

initial numbers in each age class, the numbers in the first age class each year, and the age-specific survival rates  $\{N_{1,1}, \dots, N_{1,A}, N_{2,1}, \dots, N_{T,1}, \varphi_1, \dots, \varphi_{A-1}\}$ , where  $T$  is the number of time periods and  $A$  is the maximum age in the model.

The release and recapture data comprise releases at age  $\{R_1, \dots, R_A\}$  that were released at time  $t = 1$  and recaptures at time and age  $\{m_{2,2}, \dots, m_{T,A}\}$ . The numbers of marked individuals are modeled with the same dynamics equation as the total population with removal of the marked animals that are observed  $M_{t+1,a+1} = M_{t,a} \varphi_a - m_{t,a}$ . The initial numbers at age in the marked population are set to the number of releases multiplied by the age-specific marking related mortality,  $M_{1,a} = R_a u_a$ . The parameters of the mark-recapture model to estimate are  $\{\varphi_1, \dots, \varphi_{A-1}, u_1, \dots, u_A\}$ . Finally, the sampling effort is used to predict the numbers at age examined for marks. The predicted number of individuals examined for marks is  $\hat{C}_{t,a} = E_t q_a N_{t,a}$ , where  $E_t$  is the sampling effort expended in time  $t$  and  $q_a$  is the age-specific catchability parameter. The parameters estimated to predict the number of individuals examined for marks are  $\{N_{1,1}, \dots, N_{1,A}, N_{2,1}, \dots, N_{T,1}, \varphi_1, \dots, \varphi_{A-1}, q_1, \dots, q_A\}$ . The combined set of parameters from the population dynamics model, the mark-recapture model, and the model describing the number of individuals examined for mark includes the initial numbers at age, the recruitment for each time period, the survival at age, the age-specific catchability, and the initial mark-recapture induced mortality at age  $\{N_{1,1}, \dots, N_{1,A}, N_{2,1}, \dots, N_{T,1}, \varphi_1, \dots, \varphi_{A-1}, q_1, \dots, q_A, u_1, \dots, u_A\}$ .

There are two components to the likelihood function: (1) the mark-recapture data conditioned on the number of individuals examined for marks; and (2) the number of individuals examined for marks, given the amount of effort deployed.

The likelihood for the mark-recapture data, given the individuals examined for marks  $\{C_{2,2}, \dots, C_{T,A}\}$ , is based on the binomial distribution (i.e. an individual examined for marks is either marked or not marked). Because I have reparameterized the models so they have parameters in common, I define the probability of an individual being marked as the ratio of the number of marked individuals to the total number of individuals,  $M_{t,a} / N_{t,a}$ . Note that in this example not all age classes will have the possibility of marked individuals because releases occurred only in the first time period, and this must be taken into consideration when performing the calculations.

$$L(m_{2,2}, \dots, m_{T,A} | N_{1,1}, \dots, N_{1,A}, N_{2,1}, \dots, N_{T,1}, \varphi_0, \dots, \varphi_{A-1}, C_{2,2}, \dots, C_{T,A}, u_1, \dots, u_A) = \prod_{t=2}^T \prod_{a=2}^A \left[ \frac{M_{t,a}}{N_{t,a}} \right]^{m_{t,a}} \left( 1 - \left[ \frac{M_{t,a}}{N_{t,a}} \right] \right)^{C_{t,a} - m_{t,a}}$$

The likelihood for the number of individuals examined for marks is based on a lognormal distribution with a constant

standard deviation,  $\sigma$ , which is estimated simultaneously with the other parameters.

$$L(C_{2,1}, \dots, C_{T,A} | E_2, \dots, E_T, N_{1,1}, \dots, N_{1,A}, N_{2,1}, \dots, N_{T,1}, \varphi_1, \dots, \varphi_{A-1}, q_1, \dots, q_A, \sigma) =$$

$$\prod_{t=2}^T \prod_{a=2}^A \frac{1}{\sigma \sqrt{2\pi}} \exp \left[ -\frac{(\ln(C_{t,a}) - \ln(\hat{C}_{t,a}))^2}{2\sigma^2} \right]$$

Note that this likelihood will cause numerical problems if the observed or predicted number of individuals examined

for marks is zero. The total likelihood is the product of the two likelihood components,

$$L(m_{2,2}, \dots, m_{T,A}, C_{2,2}, \dots, C_{T,A} | E_2, \dots, E_T, N_{1,1}, \dots, N_{1,A}, N_{2,1}, \dots, N_{T,1}, \varphi_0, \dots, \varphi_{A-1}, u_1, \dots, u_A) = \\ L(m_{2,2}, \dots, m_{T,A} | N_{1,1}, \dots, N_{1,A}, N_{2,1}, \dots, N_{T,1}, \varphi_0, \dots, \varphi_{A-1}, C_{2,2}, \dots, C_{T,A}, u_1, \dots, u_A) \times \\ L(C_{2,1}, \dots, C_{T,A} | E_2, \dots, E_T, N_{1,1}, \dots, N_{1,A}, N_{2,1}, \dots, N_{T,1}, \varphi_1, \dots, \varphi_{A-1}, q_1, \dots, q_A, \sigma)$$

and this is maximized while estimating the combined set of parameters, including the standard deviation of the fit to the number of individuals examined for marks,  $\{N_{1,1}, \dots, N_{1,A}, N_{2,1}, \dots, N_{T,1}, \varphi_1, \dots, \varphi_{A-1}, q_1, \dots, q_A, u_1, \dots, u_A, \sigma\}$ . I used this method to analyze the snail data set. More complex dynamics, multiple releases, different likelihood functions, or additional data types can also be modeled (e.g. Maunder, 1998; 2001b).

### 3. Bayesian analysis

Bayesian analysis is a convenient method to include prior information into models and to represent parameter estimation uncertainty. Bayesian analysis can be considered as a traditional PVA (Boyce, 1992) that includes a sensitivity analysis and is fit to data. In a PVA, estimates of the model parameters are generated with data outside the population dynamics model (e.g. estimating survival with mark-recapture data). For some parameters (e.g. initial numbers at age), fixed values are used, and for other parameters (e.g. survival) the distribution of estimated values are used so as to include stochastic variation in the forward projections. Sensitivity analyses are carried out with alternative values for the parameters that have fixed values. If the sensitivity analyses are repeated numerous times with the values for the fixed parameters drawn from the distribution of estimates, this is equivalent to including prior information on parameters in a Bayesian context. An additional aspect of a Bayesian analysis is that each realization is weighted by how well it fits the data (e.g. the fit to a relative abundance time series), rather than giving each realization of the stochastic projections equal weight. This requires simulation over the historical timeframe and into the future. Traditionally, PVAs have ignored trend data. Fitting to a time series of abundance helps estimate the correlation between parameters. For example, low biomass and high survival or high biomass and low survival may be possible, but not high biomass and high survival or low biomass and low survival. A simple method to implement a Bayesian analysis is to place the likelihood of the fit to the data of each realization into a bin. Each bin represents a range of values of the quantity of interest, and the sum of the likelihood within each bin represents the relative probability for the range of values represented by that bin (Maunder et al., 2000). In addition to the parameter uncertainty, process error in demographic parameters such as survival and recruitment can be incorporated into forward projections.

In formal terms, the posterior distribution of the parameters, given the data,  $P(\theta|data)$ , that are used for inference, is proportional to the likelihood of the data given the parameters,  $L(data|\theta)$ , multiplied by the prior probability of the parameters before the data were observed,  $P(\theta)$ . This is modified by the probability of the data,  $P(data) = \int L(data|\theta)P(\theta)d\theta$ , to ensure that the posterior distribution integrates to one.  $P(\theta|data) = \frac{L(data|\theta)P(\theta)}{P(data)}$ .

A simple introduction to Bayesian analysis in an ecological context can be found in Hilborn and Mangel (1997).

I implemented the Bayesian analysis with the Markov Chain Monte Carlo (MCMC) method. MCMC is implemented in ADMB, and is more efficient than the simple method described above. The details of MCMC and other methods used to implement Bayesian analysis can be found in Punt and Hilborn (1997). All priors that do not have information to create them are either uniform or uniform on a log scale. This is a lazy attempt to provide priors that are uninformative; however, uniform priors are often informative about some quantities of interest, and the sensitivity of results to the prior distributions should be investigated (see Punt and Hilborn, 1997 for a discussion of the use of informative and uninformative priors). Each step of the MCMC algorithm samples a value for each of the model parameters from the posterior distribution,  $P(\theta|data)$ . The model parameters can be used to calculate any derived values or to perform forward projections. By performing multiple steps of the MCMC algorithm, the distribution of the quantities of interest from these steps can be used as an estimate of the posterior distributions for those quantities.

For each set of parameters sampled with the MCMC procedure, which describes the current population size and structure and the dynamics of the system, the population model is projected forward in time with a new set of random numbers for the process error (e.g. random variation in births or survival). The quantities of interest (e.g. the ratio of the population size at the end of the projection period to the population size at the beginning of the projection period) are saved and the procedure repeated for each sample from the MCMC algorithm (or a subset of the samples to reduce correlation). The quantities of interest that are saved can then be used to describe the distribution of these values. For example, the probability that the population will decline over the projection time period is equal to the number of samples for which the population size at the end of the projection period is less than that at the beginning of the projection period divided by the total number of samples.



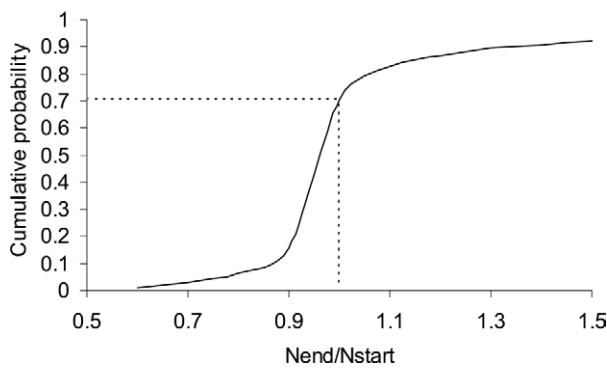


Fig. 2. The cumulative probability of the population size after 60 years ( $N_{end}$ ) as a ratio of the population size at the start of the projection ( $N_{start}$ ) for the snail data set.

Extinction is often calculated as arbitrarily occurring when the adult population size is reduced below a certain number of individuals.

An informative prior was used for the survival rate in the analysis of the snail data set. The information provided was that snails in captivity had an annual survival rate of 0.8. I assumed that the prior was normally distributed, with a mean of 0.8, an arbitrary standard deviation of 0.2, and limited to the range 0–1.

$$P(\varphi) = \frac{1}{\sqrt{2\pi} \cdot 0.2} \exp \left[ -\frac{(S-0.8)^2}{2(0.2^2)} \right] \quad 0 \leq \varphi \leq 1$$

A prior that is limited to the range of 0–1, such as the beta or logit-normal, is more appropriate for survival parameters.

A cumulative probability graph can be used to determine the probability of the population declining below a certain size. For example, Fig. 2 shows that there is about a 70% probability that the snail population will decline in abundance over the next 60 years.

#### 4. Hierarchical analysis

Models are only a simplification of reality, and there are many ways in which the model can misrepresent the real population. This is often called process error. One type of process error is random change in parameter values over time. It is important to include this variability in forward projections because stochastic variation can modify the probabilities of decline or extinction. One method to estimate this variability is to estimate an independent parameter for each time period, and then sample either parametrically or non-parametrically from the estimates and use these samples in the projections. However, there is often insufficient information in the data to reliably estimate a parameter for each time period, or there is so much uncertainty in some of the estimates that the variation is driven primarily by estimation uncertainty. The most appropriate method is to define the parameter as a random variable or, equivalently, a random-effect. This requires defining a distribution for the parameter

and estimating the parameters of this distribution during the estimation procedure. The distribution is often called the hyperdistribution, and the parameters describing the distribution called the hyperparameters (Gelman et al., 1995). The value of the parameter for each year comes from this distribution. The appropriate method of estimation uses a marginal likelihood that integrates over the parameter for each year. Fortunately, this is automatically carried out if Bayesian integration is used as the estimation procedure (e.g. McAllister et al., 1994). However, most fisheries stock assessments fix the variance of the distribution, and do not use a marginal likelihood (this is often referred to as a penalized likelihood, e.g. Maunder and Starr, 2001). The estimated hyperdistribution can be sampled to add process error in the forward projections.

One advantage of the random-effect approach is that it is often possible to estimate the variation due to parameter estimation uncertainty (observation error) separately from stochastic variation in parameters (process error). Estimation of these two types of variation reduces the contamination of the estimates of stochastic variation in demographic parameters by parameter estimation uncertainty. Separating the two types of variation also indicates what portion of the uncertainty can be reduced by collecting additional data to reduce estimation error. Methods used to implement the random-effects models estimate both the standard deviation (or related parameter) of the random-effects distribution and the standard deviation of the likelihood function (or effective sample size) and can be quite complex (e.g. Maunder and Deriso, 2003).

In Bayesian analysis, the random-effects model can be implemented with a hierarchical approach. In practice, this is implemented by penalizing the estimates of the parameters for each year. In fisheries, the most common parameter to treat as a random-effect is recruitment, which is usually defined as the number of individuals in the first age-class of the model at the start of each time period. For simplicity, recruitment is the only process error I have included in my applications to the simulated data. However, other parameters, such as survival, can be modeled by the same method. See Maunder and Deriso (2003) for more details.

Recruitment is defined as average recruitment,  $\mu_R$ , multiplied by the deviate from the average for that time period,  $\varepsilon_t$ . It is common in fisheries to assume, that recruitment is lognormally distributed, and this is implemented by using the exponent of a normal deviate with a lognormal bias correction term,  $-0.5\sigma_R^2$ .

$$R_t = \mu_R \exp(\varepsilon_t - 0.5\sigma_R^2).$$

The penalty on the deviate is included in the total likelihood (which now becomes proportional to the posterior probability), and can be considered a prior.

$$P(\varepsilon | \sigma_R) = \prod_i \frac{1}{\sqrt{2\pi}\sigma_R} \exp \left[ -\frac{\varepsilon_i^2}{2\sigma_R^2} \right],$$

where  $\sigma_R$  is the standard deviation of the temporal recruitment deviations and is a parameter included in the Bayesian integration. In a penalized likelihood context, the objective function to be maximized is

$$L(data | \theta)P(\varepsilon | \sigma_R)$$

with both  $\varepsilon$  and  $\theta$  estimated, but usually with  $\sigma_R$  fixed. However, as mentioned, a more appropriate method is to integrate across the random-effects  $\varepsilon$  and estimate  $\sigma_R$  as described below.

During the forward projection part of the Bayesian procedure the same equation,  $R_t = \mu_R \exp(\varepsilon_t - 0.5\sigma_R^2)$ , is used to represent recruitment with each deviate,  $\varepsilon_t$ , being a random number from  $N(0, \sigma_R^2)$ .

When using full Bayesian integration, priors are required for the hyperparameters. These priors are called hyperpriors (Gelman et al., 1995). In formal terms, the posterior distribution of the parameters,  $\theta$ , and the hyperparameters,  $v$ , given the data,  $P(\theta, v | data)$ , which is used for inference, is proportional to the likelihood of the data given the parameters,  $L(data | \theta)$ , multiplied by the probability of the parameters given the hyperparameters  $P(\theta | v)$ , multiplied by the prior probability of the hyperparameters before the data were observed,  $P(v)$ . This is modified by the probability of the data,  $P(data) = \iint L(data | \theta)P(\theta | v)P(v) d\theta dv$ , to ensure that the posterior distribution integrates to one.

$$P(\theta, v | data) = \frac{L(data | \theta)P(\theta | v)P(v)}{P(data)}$$

For the example using a random-effect for the annual recruitment anomaly,  $v = \sigma_R$  and  $\theta = \{\varepsilon_1, \dots, \varepsilon_T, \theta_1, \dots, \theta_n\}$  where  $\theta_1, \dots, \theta_n$  are the other model parameters. The parameters represented by  $v$  and  $\theta$  are all estimated in the Bayesian analysis.

When parameters of the population dynamics models have trends or are related to environmental factors, it has been suggested that the most appropriate method is to integrate the trend or environmental factor into the analysis and use random-effect models (Link, 1999; Maunder and Waters, 2003). This reduces bias caused by estimation error, provides additional information to estimate the model parameters, and improves the performance of hypothesis tests. For example, if recruitment is related to an environmental variable  $I$ ,  $R_t = \mu_R \exp(\alpha + \beta I_t + \varepsilon_t)$ , where  $I_t$  is the value of the environmental time series at time  $t$  and the parameter  $\alpha$  ensures that  $\mu_R$  is equal to the mean over the whole time period. Therefore,  $\alpha$  removes the lognormal bias and bias caused by an unnormalized environmental time series,

$$\alpha = \ln \left( \frac{T}{\sum \exp(\varepsilon_t + \beta I_t)} \right),$$

where  $T$  is the number of time periods and the penalty on the annual deviates,  $P(\varepsilon | \sigma_R)$ , described above, is included in the total likelihood (posterior).

## 5. Non-parametric parameter representation

It is common in fisheries modeling to represent parameters that may change over time, or with some other characteristic (e.g. age), by a functional form. This is because the information in the data is insufficient to reliably estimate all the values as independent parameters, and parameters that represent characteristics that are similar (e.g. consecutive years or ages) are expected to be similar. For example, vulnerability to the fishing gear at age is often represented by the logistic function. However, these functional forms are often insufficiently flexible to represent the parameters and may be inappropriate for a particular application, leading to biased results (Haist et al., 1999).

Fournier et al. (1998) suggested using a non-parametric approach to represent the function form. This method involves estimating the parameters as separate values, but including a smoothing penalty so that parameters representing characteristics that are similar have similar values (see Haist et al., 1999). The penalty helps avoid overparameterization of the model. In fisheries applications, these smoothing penalties are often based on the difference equation approximation to the first, second, and/or third derivatives of the curve. The first difference,  $\lambda_1 \sum_{i=1}^{i=n-1} [\theta_i - \theta_{i+1}]^2$ , penalizes the objective function if the parameter is not constant, the second difference,  $\lambda_2 \sum_{i=1}^{i=n-2} [\theta_i - 2\theta_{i+1} + \theta_{i+2}]^2$ , penalizes the objective function if the relationship among parameters is not linear, and the third difference,  $\lambda_3 \sum_{i=1}^{i=n-3} [-\theta_i + 3\theta_{i+1} - 3\theta_{i+2} + \theta_{i+3}]^2$ , penalizes the objective function if the relationship among parameters is not parabolic. The  $\lambda$ s determine the strength of the penalties. If  $\lambda$  is large the penalty will act more like a constraint.

A penalty can also be used to make the relationship among parameters monotonically increasing,  $\lambda_{\text{mon}} \sum_{i=1}^{i=n-1} I(\theta_i > \theta_{i+1}) [\theta_i - \theta_{i+1}]^2$ , where  $I(\cdot)$  is an indicator function that equals 1 when the inequality is true and 0 otherwise. It may be used to create desired characteristics. The smoothness penalties described above are applied to the objective function when it is in the form of a negative log-likelihood, so the value needs to be negated and then exponentiated before combining it with a likelihood function.

I used the non-parametric representation of parameters to define the initial numbers at age and the survival rate at age for the small mammal population. I base the penalties on the logarithm of the selectivity parameters to avoid scale-related problems and improve the stability of the estimation procedure (James Ianelli, US National Marine Fisheries Service, Seattle, USA, personal communication).

The smoothness penalty on the survival parameters was implemented as a first difference.

$$\lambda \sum_{a=1}^{a=8} (\ln(\varphi_a) - \ln(\varphi_{a+1}))^2.$$

The initial numbers at age  $a$  were penalized for being different from the initial numbers at age  $a - 1$  multiplied by survival for age  $a - 1$ . The oldest age-group was modeled as a plus group that accumulates all individuals age nine and older and the algebraic representation of the summation over an infinite number of older age-classes was used.

$$\lambda \left( \ln(N_{1,9}) - \ln(N_{1,8}\varphi_8/(1-\varphi_9)) \right)^2 + \lambda \sum_{a=1}^{a=7} \left[ \left( \ln(N_{1,a+1}) - \ln(N_{1,a}\varphi_a) \right)^2 \right],$$

where  $N_{t,a}$  is the number of age- $a$  individuals at time  $t$  and  $\varphi_a$  is the annual survival rate of individuals of age  $a$ . The objective function was formed by adding the penalties described above to the negative log-likelihood. For Bayesian analysis this objective function is negated and then exponentiated to form the posterior probability.

One remaining area of research is methods to determine the weighting factors for smoothness penalties. As might be expected, different weighting factors can lead to different results in some applications. Maunder and Harley (2003) used cross validation to investigate appropriate weighting factors for age-specific selectivity parameters of a fisheries stock assessment model.

## 6. Robust likelihood functions

Data from natural populations often have more extreme values than expected from standard statistical theory (Fournier et al., 1990). These data points could be due to several sources of error (e.g. inaccurate recording of results) or rare processes that are not important to the overall dynamics and may have an undue influence on the results. In applications with only a few data points, these extreme values can be removed from the analysis to determine their influence on the results. Unfortunately, due to the large amount of data often used in integrated analysis (e.g. Fournier et al., 1998), this is not possible. Therefore, automatic methods are required to downweight extreme values or remove them from the analysis. One method is to modify the likelihood functions so that outliers do not have a large influence on the results. This is achieved by assuming that the data come from two distributions, one that describes the majority of the data and a heavier-tailed distribution that describes the outliers (Fournier et al., 1990). The heavier-tailed distribution describes the contamination in the data. Fournier et al.'s (1990) robust likelihood function adds 0.01 to the normal likelihood, which ensures that the influence of observations reduces rapidly as their distance from the predicted value becomes greater than about three standard deviations.  $L_{\text{robust}}(\text{data} | \theta) = L(\text{data} | \theta) + 0.01$ . Other formulations of robust likelihoods that may be more appropriate for certain applications are also available. Simulation analysis has shown that these robust likelihood functions perform only slightly worse than a standard likelihood function for which there are no outliers, but perform substantially better when outliers are present (Chen et al., 2000).

## 7. Implementation in AD Model Builder

AD Model Builder (ADMB, Otter Research, <http://otter-rsch.com/admodel.htm>) is becoming the predominant programming environment for producing complex highly-parametrized fisheries stock assessment models (see Maunder, 2000, for a review), particularly for researchers working in the west coast of North America and in the south Pacific.

ADMB is a set of libraries for C++ and a template to simplify setting up the model. ADMB uses the C++ library AUTODIF, which calculates the derivatives of all the operations analytically. (AUTODIF has precompiled adjoint code for the derivatives of commonly-used array and matrix operations and the reverse mode of automatic differentiation for other operations). The exact derivatives make the minimization procedure more efficient and stable. Most modern statistical modeling packages use finite difference approximations for these derivatives, leading to two major limitations. First, the inaccuracy of the derivative approximations causes instability in the minimization process and produces unreliable results for ill-conditioned problems. Second, finite difference approximations take  $n+1$  function evaluations to obtain the finite difference approximation for a function with  $n$  independent variables. In contrast, ADMB can compute exact values for the derivatives at the same time as it evaluates the function. This additional computation requires only about four times as much time as it takes to calculate the function itself, resulting in a substantial saving of time relative to the approaches that use the finite difference approximation. Schnute et al. (1998) showed that ADMB was significantly superior to the statistics packages GAUSS, MATLAB, and S-Plus, which use finite difference approximation, for estimating the parameters of a catch-at-age model. ADMB took only 3% of the time of the next-best package for a 37-parameter model and less than 1% of the time for a model with 100 parameters. Therefore, ADMB is more appropriate for the implementation of integrated analyses that have large amounts of data and numerous parameters to estimate.

The template used in ADMB allows for definition of data to be read in, definition of estimated parameters, and formatting of output. The template also sets up all the code needed to carry out the estimation. All the underlying code used to define the model and objective function is coded in C++ (mainly C). Therefore, ADMB is very flexible, and allows experienced C++ programmers to create their own libraries that can be used in conjunction with the ADMB libraries.

ADMB provides a flexible stepwise process to sequentially estimate the parameters, and allows the placing of bounds on all estimated parameters that restrict the range of possible parameter values. ADMB also contains automation of likelihood profiles and a MCMC algorithm for Bayesian integration. The MCMC algorithm implemented in ADMB has jumping rules that are based on the variance-covariance estimated at the mode of the joint posterior distribution and starts at the mode of the joint posterior, which makes the algorithm more efficient (i.e. reduces the burn-in time).

Other software is available that can be used to carry out the analyses presented here. One popular program is BUGS (Spiegelhalter et al., 1995), which has been used to perform Bayesian analysis for fisheries and wildlife applications (e.g. Meyer and Millar, 1999; Link et al., 2002).

## 8. Discussion

I present several methods used in fisheries stock assessment models that can be applied to population viability analysis. Integrated analysis allows the use of all information on a particular population, ensures that all model assumptions and parameters are consistent throughout the analysis, that uncertainty is propagated throughout the analysis, and that the correlation among parameters is preserved. Bayesian analysis allows for the inclusion of prior information, and is a convenient way to represent uncertainty. Random-effects modeling allows information to be shared among parameter estimates, and allows the separation of process error from estimation error. Non-parametric representation of parameters allows for a more flexible relationship among the parameters, while still avoiding overparameterisation. Robust likelihood functions provide an automatic method to reduce the effects of outliers when the data sets used are large.

Bayesian analysis and integrated analysis provide a comprehensive framework for including all available information (priors and data) into a single analysis and the representation of uncertainty. Due to uncertainty, management decisions have multiple possible outcomes, so it is important for management to know the probabilities of the outcomes of the various management decisions that are under consideration. Because Bayesian analysis produces these probabilities, it is an appropriate method for analysts to use for providing management advice. For example, management of the New Zealand sea lion population involves closing a squid fishery if too many sea lions are caught by the fishery in a given year. Maunder et al. (2000) used Bayesian analysis to determine the effect of different sea lion mortality limits on both the sea lion population and the squid catch. Decision makers were presented with the probability that the sea lion population would rebuild and the expected loss in squid catch so that they could make an informed decision based on the tradeoff between these two factors. The analysis also makes it clear to all user groups what the tradeoff is, rather than just setting conservative criteria.

When stochastic variation in demographic parameters is a central component in determining the probability of extinction or population decline, it is important to provide accurate estimates of the variation that will be used in the forward projections. Therefore, the analyst must separate the true variation in the demographic parameters from the estimation uncertainty. The estimation uncertainty comes from the frequent problem that there is insufficient information in the data to estimate the parameter for each time period. If the estimates of the parameter for each time period are used to

determine the temporal variation in that parameter, the temporal variation will be biased upward because it includes both the temporal variation and the estimation error (Maunder and Deriso, 2003). An appropriate method to separate the temporal variation from the estimation error is the random-effects approach, which is becoming popular in fisheries and wildlife modeling (e.g. Link, 1999; Maunder and Deriso, 2003).

The methods presented here all appear reasonable, and it would be beneficial to employ them all for conservation biology applications. However, due to the complexity of the models and the large data sets, these analyses are often difficult to apply. They can require large amounts of computer memory and CPU time. Often there are multiple local solutions. Sometimes, Bayesian integration methods do not perform well. Model selection becomes difficult because multiple data types are combined and different weighting among data sets can produce different answers. In addition, diagnostics for complex non-linear models are relatively undeveloped, compared to those for linear models. These issues should be addressed in future research.

The recent developments in fisheries stock assessment that I have presented are also beginning to be used in conservation biology. Bayesian analysis has been used for several conservation biology applications (see Ecological Applications volume six number four for a special section on Bayesian methods) including PVA (Ludwig, 1996; Taylor et al., 1996; Goodman, 2002; Wade, 2002; Breen et al., 2003). Random-effects models have been used to determine individual heterogeneity in breeding and survival rates (Link et al., 2002), temporal variability in survival rates (Burnham and White, 2002), and population trends (Sauer and Link, 2002). White and Lubow (2002) described methods to fit population models to multiple sources of data. Integrated analysis has been used to model patterns in collections of parameters in a random-effects context (Link, 1999). It appears that the modeling methods used in conservation biology and fisheries stock assessment are converging, and may provide a general framework for all ecological modeling as promoted by Shea (1998).

The four artificial data sets created by the Extinction Risk Working Group of the National Center for Ecological Analysis and Synthesis (NCEAS) are examples of different types of situations that are experienced when modeling populations. The frog data are from a population whose estimated parameters are uncertain, whereas the snail data are from one for which the parameters are well estimated and there is little annual variability. Neither of these populations show a decline in population size. In contrast, the herb and small mammal populations show declining trends. The snail population was estimated to have a zero probability of extinction because there is no declining trend in abundance, low inter-annual variability, and low uncertainty in parameter estimates. The frog population was estimated to have a small probability of extinction due to uncertainty in parameter estimates. The herb and small mammal populations were



estimated to have high probabilities of extinction because of the declining trends in abundance. However, the true populations did not have trends in abundance. This indicates that detecting trends in abundance, in this case through trends in birth rates, is an important factor in estimating the probability of extinction. Therefore, predicting trends in model parameters and correlating them with measurable variables (e.g. habitat size) is an important requirement for conservation modeling. Random-effects models appear to be the most appropriate method to model these trends and correlations (Link, 1999; Maunder and Watters, 2003; Maunder and Deriso, 2003). Fisheries models differ from most conservation models because the catch, which is a main component that causes decline in population size, is often recorded reasonably accurately. Therefore, it is easy to investigate the effect that catch has on the probability of decline. However, for conservation problems, the reasons for decline are often unknown or, if known, difficult to obtain data for. Therefore, it is difficult to determine the effect that this factor has on the probability of decline or extinction.

Risk of extinction in these models was based on parameter uncertainty, annual variability in recruitment, and, in the case of the herb and small mammal applications, trends in biomass. In many populations, catastrophes are the most likely cause of extinction. In these cases, looking at the probability distribution of catastrophes and the distribution of catastrophe effects may be a better method to determine extinction (Gerber and Hilborn, 2001). Breen et al. (2003) included catastrophes in a Bayesian and integrated analysis of New Zealand sea lion.

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