$$E[R|S] = S \times \alpha \times f(S|S_{EQ})$$

where R = production of adults in subsequent generation, S = abundance (escapement) of adults, α = intrinsic rate of increase, and S_{EQ} = carrying capacity (Figure 1).

In this simple model, there is an intrinsic rate of increase (α) due to the average per-adult generation of ova and the survival of these ova to adult in the absence of competition. Counteracting this rate of increase is a discount due to competition, $f(S|S_{EQ})$, that increases as escapements tend towards a theoretical carrying capacity (i.e., average escapements in the absence of fishing mortality or S_{EQ}).

The intrinsic rate of increase, also known as the density independent parameter, is thought to be species and also regionally specific. Factors influencing the intrinsic rate of increase are variability in life history characteristics such as fecundity, maturation rate, growth rate as well as environmental influences on survival in fresh and salt water.

Carrying capacity is thought to be watershed specific and can be effectuated via rearing or spawning ground limitation. Rearing limitation in Pacific salmon is thought occur as competition among juveniles for food or space in the freshwater rearing environments of some species. Evidence of these limitations can be seen in variation in time spent residing in freshwater or in size of juveniles at the time of smoltification. Spawning ground limitation is thought to occur as adults compete for suitable spawning areas. Evidence of these limitations can be seen in variation in the location and density of redds and in the amount of egg retention in adults due to competitive interactions.

Several specific production models have been postulated for Pacific salmon. The main difference in these models is the mathematical formulation of compensation in survival rates (R/S) as competition increases. Two common models for compensation in survival rates are: 1) asymptotic (*S/R* increases linearly) or 2) exponential (*ln*(*R/S*) decreases linearly) as spawning abundance increases. In relation to the generic production model above, the differing forms for discounting due to competition are:

$$f(S|S_{EQ}) = \frac{1}{1+\frac{(\alpha-1)}{S_{EQ}}S} \text{ or } f(S|S_{EQ}) = exp\left[-\frac{ln(\alpha)}{S_{EQ}}S\right].$$

These two mathematical forms result in the two most common production models for Pacific salmon: 1) Beverton-Holt (Beverton and Holt 1954) and 2) Ricker (1975; Figure 2). The Beverton-Holt model can be used to model competition due to rearing or spawning limitation, whereas the Ricker model can only be used to model spawning limitation (see Quinn and Deriso 1999). The Beverton-Holt model can only exhibit simple or pure compensation, where the expectation of maximum production occurs at carrying capacity. Over-compensation can occur in the Ricker model, where the expectation of maximum production can occur at intermediate levels of escapement depending on the intrinsic rate of increase.

Although choice of production model represents one form of scientific uncertainty that could be accounted for in escapement goal development, Alaska has largely chosen to use the Ricker model. Reasons for extensive use of the Ricker production model in Alaska are both biological and practical. Production in most Pacific salmon stocks in Alaska is arguably driven by competition among adults on the spawning grounds. Biological evidence for competition among adults can be seen in egg retention from overcrowding on spawning grounds, dominance of a age-1 smolts when harvest rate (and competition) is low, size of juveniles is not inversely related to parent escapements when harvest rate is low, and little or no rearing of juveniles in freshwater (i.e., for chum and pink salmon).

Empirical evidence for a Ricker production model comes from dome-shaped production plots, superior statistical fits to Ricker versus Beverton-Holt production models, and poor production from exceptionally large escapements for various stocks in Alaska, indicating that maximum production occurs when escapements are held at an intermediate level in relation to carrying capacity (see Clark et al. 2007 for examples). Moreover, many stocks of Pacific salmon in Alaska consistently provide surplus production (i.e., meet and exceed lower bound escapement goals) under moderate to high harvest rates, arguable evidence of a dome-shaped production relationship.

From a practical standpoint, use of the Ricker production model will consistently provide for precautionary management under a fixed escapement goal management paradigm. Assuming fixed intrinsic rate of increase and carrying capacity, the Ricker model will provide a lower average harvest rate and higher average escapement than the equivalent Beverton-Holt model (Figure 3).

Incorporation of Uncertainty into Production Models

Two general forms of uncertainty are accounted for in production models used to develop escapement goals in Alaska. Process error is the uncertainty in production introduced by variation in survival rates from ova to adult. Biological mechanisms for process error in Pacific salmon include variation in sex ratio, fecundity, growth (size composition), maturation (age composition). Environmental mechanisms for process error include variation in freshwater habitat (e.g., stream flows, stream temperature) as well as marine habitat (e.g., ocean temperature and circulation patterns). Ecosystem linkages can also create process error in survival rates in the form of predation, inter-specific competition, disease, and starvation for example.

Process error can be easily introduced into a production model as density-independent and stochastic. For example, the Ricker production model has the stochastic version:

$$E[R|S] = exp\left(ln(\alpha) - \frac{ln(\alpha)}{S_{EQ}}S\right)\exp\left(\frac{\sigma_{\varepsilon}^{2}}{2}\right),$$

where σ_{ε}^{2} is a log-normally distributed random variable (Peterman 1981) that represents variation from the expectation due to process error. Serially correlated patterns of lag-1 are often seen in process error in Pacific salmon, so that an alternative process error model is used:

$$E[R|S] = exp\left(ln(\alpha) - \frac{ln(\alpha)}{S_{EQ}}S\right)\exp\left(\frac{\sigma_{\varepsilon}^{2}}{2(1-\phi_{1}^{2})}\right),$$

where □$_1$ is the lag-1 correlation coefficient. Random walk Kalman filtering has also been used to assess serially correlated process error in salmon production (Peterman et al. 2003).

Another form of uncertainty in production models comes from measurement errors introduced into the annual stock assessment process. Escapements are routinely estimated rather than counted using weirs, sonar, mark-recapture, aerial survey, or a combination of methods to reconstruct runs. In many cases measurement error in escapements are small (e.g., complete counts at weirs) and can be ignored in development of an escapement goal. However, high measurement error in escapements can create bias in estimates of the intrinsic rate of increase that is high or low depending on the magnitude of harvest rates (Kehler et al. 2002). This bias can directly affect development of an escapement goal. Age composition of annual runs are routinely estimated from a sample of catches and escapements. Catches are also estimated with error, especially when sport or subsistence harvests are substantial and or commercial harvests in mixed-stock fisheries are estimated from stock identification techniques such as genetic stock identification.

Time series bias can also enter into the escapement goal development process (Walters 1985). Data that are used to estimate to develop production models usually come from annual stock assessments where the escapements in one year are not independent of escapements in proceeding years. This can confound the estimation of the relationship between escapements and production and bias estimates of intrinsic rate of increase and carrying capacity.

When necessary, uncertainty in the form of measurement errors in escapements, catches, age compositions, and other types of run reconstructions can be incorporated into the production model. Time series bias can also be accounted for in these same models. As described below Alaska currently utilizes methods of escapement goal analysis that bring all of these sources of uncertainty into "full probability" state-space models.

Escapement Goal Analysis

Management parameters can be estimated directly from the production models described above. For example the Ricker production model leads to the following estimates of interest to escapement goal development for Pacific salmon (from Hilborn 1985):

$$S_{MSY} \cong S_{EQ}\left(0.5 - 0.07ln(\alpha')\right),$$

where, S_{MSY} is the escapement that maximizes sustained yield on average (*MSY*) and $ln(\alpha') = ln(\alpha) + \frac{\sigma_\varepsilon^2}{2}$ for the log-normal random process error model. Harvest rate at *MSY* (U_{MSY}) can also be estimated in this way:

$$U_{MSY} \cong ln(\alpha')\big(0.5 - 0.07ln(\alpha')\big).$$

MSY is then calculated by plugging S_{MSY} back into the Ricker equation:

$$MSY = S_{MSY}\left(\exp\left(\ln(\alpha') - \frac{\ln(\alpha')}{S_{EQ}}S_{MSY}\right) - 1\right).$$

The limiting rate of exploitation (that drives the stock to extinction) can also be calculated directly from α':

$$U_{lim} = 1 - \frac{1}{\alpha'}.$$

Escapement goals in Alaska are developed directly from these management parameters or their proxies. Moreover, these goals are commonly specified as ranges (see Munro and Volk 2010). Although no specific standard has been set in policy, Alaska has generally developed these ranges based on the premise that when fisheries are managed to keep escapements within the goal range, the targeted stock would produce 90 percent or more of *MSY*. Use of ranges takes advantage of the fact that the Ricker production model provides relatively similar yields across a wide range of escapements close to S_{MSY}. Use of ranges also addresses uncertainty in implementing fixed escapement goal management of Pacific salmon fisheries, where preseason forecasts of run strength are often imprecise and knowledge of realized run strength improves as the fishery proceeds.

Proxies for S_{MSY}

Empirical development of production models require time series of data on escapements and resultant production. In many cases in Alaska available fishing power is insufficient to cause overfishing (i.e., resultant escapements below the lower bound of the escapement goal), average harvest rates are generally lower than U_{MSY}, and management is largely predicated on a schedule of fixed duration fishery openings. In other cases in Alaska, there are mixed-stock and mixed-species fisheries where catches cannot be resolved by stock during the fishing season. In these fisheries, stock-specific production data are usually lacking, but a time series of post-season escapement data are available to develop an escapement goal.

Based on these realities, Alaska has developed several proxies that are based on production theory, knowledge of fishing power and relative harvest rates, and the ability (or inability) to manage fisheries in-season. Most lower bound SEG and SEG ranges are based on these proxies (Munro and Volk 2010).

Classical methods of stock-recruit analysis usually involve linear transformation of the production model and following the linear regression recipe to estimate the parameters of interest (Ricker 1975). Recasting the stochastic Ricker production model in the following way:

$$R = Sexp(ln(\alpha) - \beta S)\exp(\varepsilon), \text{where } \beta = \frac{ln(\alpha)}{S_{EQ}},$$

and then dividing by S and log-transforming so that

$$ln\left(\frac{R}{S}\right) = ln(\alpha) - \beta S + \varepsilon,$$

allows for the simple linear regression of $ln\left(\frac{R}{S}\right)$ on S to estimate $ln(\alpha)$ as the y-intercept and β as the slope. The residual error of the regression provides the estimate of ε. Management parameters can then be estimated in the usual way with $E[\varepsilon] = \frac{\sigma_{\varepsilon}^2}{2}, ln(\alpha') = ln(\alpha) + \frac{\sigma_{\varepsilon}^2}{2}, and\ S_{EQ} = \frac{ln(\alpha')}{\beta}$.

Escapement goals (BEGs and SEGs) for many stocks in Alaska were developed using this method (see Fried 1994, Clark 2001, Bue and Hasbrouck Unpublished, and Geiger 2003 for examples). Ranges around the point estimate of S_{MSY} were calculated in a variety of ways, but most commonly using the range that produces 90 percent or more of the point estimate of *MSY* or by applying the results of simulation work by Eggers (1993). Eggers simulated yields from a Ricker production model along with implementation error in management and found that an escapement goal range that was 0.8 to 1.6 times the point estimate of S_{MSY} provided for average yields that were 90% or more of the point estimate of *MSY*.

More recently salmon biologists in Alaska have used probabilistic approaches to the classical method of stock-recruit analysis and extended the analysis to provide information on sustained yield, yield in relation to MSY, and overfishing. These methods include bootstrapping of the linear regression recipe (see Clark and Clark 1994, Bernard et al. 2000, Clark and Etherton 2000, and McPherson and Clark 2001 for examples) and maximum likelihood estimation of the management parameters (e.g., Fair et al. 2004 for Kvichak River sockeye salmon). In addition to point estimates of the management parameters, these methods provide estimates of uncertainty distributions of these parameters. In particular, Alaska has developed probability profiles for attainment of 90% or more of MSY (Szarzi et al. 2007) and for overfishing (probability of low escapements producing less than 90% of MSY (Bernard and Jones 2010)). These profiles are useful for determining and defending escapement goal ranges that are robust to uncertainty in the management parameters (Figure 7). These methods continue to be used in Alaska in situations where escapement is measured with little to no error, harvest rates are low to moderate, and there is no serial correlation in residuals (e.g., Fair et al. 2008 for Eshamy Lake sockeye salmon).

Although probabilistic approaches to classical methods are an improvement in escapement goal analysis, potential for bias in the management parameters due to: measurement error in estimates of escapement; non-independent estimates of escapement through time; and, serially correlated residual errors remain. To address these potential biases, Alaska has developed Bayesian state-space models of production for Pacific salmon (Meyer and Millar, 2001), especially for situations where escapements are estimated with error (e.g., mark-recapture) and stock assessments are the result of a wide range of sampling programs each with sampling error (e.g., contributions from coded wire tag recoveries to estimate stock-specific harvest or run reconstruction to estimate escapement of a large stock complex). These models mimic the stock assessment processes used to estimate the inputs to the production model. The state-space model allows for non-independence of the time series of escapements as the process to estimate catches and therefore estimate subsequent escapements is accounted for. In the Bayesian framework, marginal posterior distributions of the management parameters are estimated using Markov Chain-Monte Carlo methods (a Gibbs sampler) as implemented in the program WinBUGS (Lunn et al. 2000).

The observation equations of the state-space model are of the general form:

$$\hat{S} = S^{true} exp(v^S) \text{ and } \hat{C} = C^{true} exp(v^C),$$

where, both escapement (*S*) and catch (*C*) are estimated with iid log-normal errors $\left(e.g., v^S \sim N(0, \tau_S^2)\right)$.

The link between successive years is accomplished by fishing (*C*) on the annual run (*N*) to produce escapement (*S*) for the next brood in year *t*:

$$\hat{S}_t = \widehat{N}_t - \hat{C}_t.$$

Subsequent production (*R*) from escapement in year *t* is estimated from annual runs and the age compositions for ages *x* to *y*, depending on the maturation schedule of the stock (e.g., *x*=4 and *y*=6 for typical Chinook salmon stocks):

$$\widehat{R}_t = \sum_{a=x}^{y} \hat{p}_{t+a,a} \widehat{N}_{t+a},$$

where the estimated age compositions $\left(p_x, p_{x+1}, \ldots, p_y\right)$ that represent the maturity schedule of a particular brood year are drawn from a $Dirichlet\left(\gamma_x, \gamma_{x+1}, \ldots, \gamma_y\right)$ distribution.

The state equation for the Ricker model is then:

$$\widehat{R} = \hat{S} exp\left(ln(\alpha) - \beta \hat{S}\right) \exp\left(\frac{\widehat{\sigma}_\varepsilon^2}{2}\right).$$