

UNCERTAINTY ANALYSIS OF STOCK RECRUITMENT RELATIONSHIPS FOR SELECTED WESTERN ALASKA CHUM STOCKS*

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1. INTRODUCTION

Use of best science, by today's standards, for managing salmon harvest, should mean employing a harvest control rule whose performance has been demonstrated to be at least as good as other practical alternative control rules in the context of a *management strategy evaluation*. Management strategy evaluation simulates performance of the candidate control rule in an *operating model* of the system consisting of the fishery, the fish stock, and its environment. Ideally, the operating model will be parametrized using all available data, weighted appropriately for the data quality, and analyzed by up-to-date statistical methods which quantify all relevant uncertainties as well as providing parameter estimates. This program of analysis is well recognized, in principle, within fisheries science, and was clearly defined and recommended by Hilborn and Walters (1992). A recent sophisticated and comprehensive theoretical treatment is given by Schnute et al. (2000).

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The standards for actually carrying out a management strategy evaluation are somewhat open-ended, depending as they do on state-of-the-art statistical techniques, exhaustive representation of relevant uncertainties, evolving understanding of the natural variability in ecological systems, uneven data availability, and an expanding appreciation for what kinds of data may in fact prove to be pertinent. Management strategy evaluations may range in their specificity from fairly generic explorations of the relative merits of some classes of control rule, to very concrete models of particular fisheries. Some published examples of management strategy evaluations include Eggers (1993), Punt (1995), Walters and Parma (1996), Butterworth and Punt (1999), and Hilborn et al (2002).

Three very important themes that should bear on updating management strategy evaluations for salmon management are the recent developments in characterizing ocean-climate variation, recent developments in predicting variation in salmon production as a function of environmental variables, and recent developments in Bayesian methods for statistical uncertainty analysis.

1.1. Ocean-climate Variation

It is now apparent that the north Pacific ocean-climate system varies in a spatially coherent way, with temporal persistence on time scales ranging from years to decades (Gershunov and Barnett, 1998; Minobe 2000; Newman et al. 2003). This manifests itself in patterns of sea surface temperature defining the Pacific Decadal Oscillation Index (Zhang et al. 1997; Mantua et al. 1997) and another possible mode of variation (Bond et al. 2003), atmospheric pressure defining the Aleutian Low Pressure Index (Beamish et al. 1997; Overland et al 1999) and the North Pacific Index (Trenberth and Hurrell 1994). These indices are correlated among themselves and with other meteorological variables (Trenberth 1990; Hurrell 1995; Gedalof and Smith 2001).

Shifts in these indices are correlated with ecological changes at various trophic levels (Mantua et al. 1997; McGowan et al. 1998; Sugimoto and Takokoro, 1998; Benson and Trites 2002; Hunt et al. 2002; Clark and Hare 2002), including, specifically, shifts in salmon productivity (Hare and Francis 1994; Beamish et al. 1999; Hare et al. 1999; Beamish et al. 2004b). Other measures of ocean productivity vary on similar time scales, but not necessarily in synchrony (Francis and Hare 1994; Polovina, 1995; Gregg, 2002), as do shifts in marine community composition (Chavez et al. 2003).

1.2. Environmental Variables and Salmon Production

It is also emerging that meteorological and/or oceanographic variables have considerable power to account for annual variation in salmon survival (Scarnechia 1981; Scheurell and Williams 2004; Lawson et al. 2004; Shotwell et al. 2004; Peterman and Haeseker 2004) though it appears that these sorts of correlations may not be stable over long durations (Myers 1998). The measures of oceanographic/meteorologic state and estimates of salmon survival rates both show spatial coherence (Meuter et al. 2002).

Notwithstanding the spatial coherence and temporal persistence of these phenomena, it appears that there is an important degree of independent stock-specificity which suggests that maintaining local diversity (and perhaps within-stock life history diversity as well) may be important to risk-spreading for the species and for the stability of harvests aggregated over stocks (Hilborn et al. 2003; Mantua and Francis 2003).

There is considerable evidence that most of the interannual variation in smolt-to-adult survival is owing to variation in the survival of juveniles during freshwater overwintering or during the first year at sea (Bradford et al. 1997; Beamish et al 2004a; and the Pacific Salmon Commission Chinook Technical Committee studies showing effectiveness of the coded-wire-tag-derived ocean survival index of indicator hatchery stocks for improving the fit to the stock-recruit models for related wild stocks).

1.3. Uncertainties in the Stock-Recruitment Relationship

Three sources of variation or error contribute to the total uncertainty in the predictions from a model. These are (1) systematic model error, (2) parameter uncertainty, and (3) process variation.

Systematic model error arises from use of the “wrong” model. The wrong model may portray a basic relationship incorrectly, or it may omit an influential variable that varies non-randomly. With sufficient data, systematic model error within the range covered by the data will be apparent from a pattern in the lack of fit. Systematic model error confined to a domain outside the range of the data will not be detectable from the fit to the data, but it may have considerable effect in simulations that explore behavior outside the range of the data.

Parameter uncertainty should be revealed directly by any adequate statistical procedure for estimating the parameters from observations. Bayesian methods are especially apt for this purpose, as they can deliver explicit distributions of

parameter uncertainty, and can deliver joint distributions for multiple parameters, which will be important to the correct calculation of the consequent uncertainty for quantities that depend on more than one of the primary parameters (Punt and Hilborn, 1997). Any predictive modeling based on the parameter estimates should propagate the parameter uncertainty. The fundamental sampling unit for parameter uncertainty in such modeling is the individual realization (e.g., the individual trajectory).

Process variation arises from the effects of unaccounted for factors that vary more or less randomly. Both process variation and random measurement error contribute to the residuals in the fit to the data. If the variance of the measurement error is known, the variance of the process variation may be calculated from the distribution of the observed residuals. Predictive modeling must also propagate the process variation, but it propagates differently from the parameter uncertainty in that the fundamental sampling unit is the process dynamical step (e.g., the time step).

1.4. Objectives of this Report

Many western Alaska chum stocks have experienced low productivity and much reduced runs in recent years, causing hardship for subsistence users. These stocks are managed under a State policy requiring that the objective be maximum sustained yield (MSY). This is implemented by attempts to manage for a fixed escapement goal. When sufficient data are available for estimation of a stock-recruit relationship, the management escapement goal is a Biological Escapement Goal (BEG), generally selected from a range calculated as 0.8 to 1.6 times the MSY spawning escapement calculated from point estimates of the respective parameters of the Ricker stock-recruitment relationship fit to the data. The rationale for this policy is that a management strategy analysis of this control rule showed reasonably good performance over a range of conditions when the operating model was in fact a Ricker stock-recruit relationship (Eggers, 1993).

The objective of the present report is to analyze the stock-recruit data for the three western Alaska chum stocks which have sufficient data to support detailed statistical estimation of the underlying parameters. These stocks are Andreafsky River summer chum, Anvik River summer chum, and Kwiniuk River chum. Each of the three stocks with long data records illustrate the region-wide productivity decline in one form or another. A subtheme of this analysis will be inquiry into the nature of the recent decline of productivity.

Systematic model error, parameter uncertainty, and process variation all play considerable roles in modeling stock-recruit relationships from actual data. This report will proceed by quantifying the pertinent uncertainties in the use of stock-recruit data for purposes of conducting a management strategy analysis and setting escapement goals for such stocks. Three aspects of the stock-recruit analysis will receive particular attention. These are (1) the uncertainty about the estimate of the escapement level that is associated with MSY, (2) the uncertainty about the recruitment rate at spawning escapements well above the unharvested equilibrium, (3) and indications of pattern in the departure of productivity from the expected level.

2. TIME SERIES PROPERTIES OF LONG TERM REGIME VARIATION

In the past few years, it has been hypothesized that the ocean/climate states reflected in the monitored indices represent a small number (possibly just two) of fairly discrete states, with characteristic probabilities of fairly abrupt transitions from one to the other, leading to characteristic persistence times of states encompassing a large number of related variables, possibly with some more or less cyclic properties (Ebesmeyer, et al., 1991; Hare and Mantua, 2000). The time span of the data sets with direct systematic and synoptic measurement of the oceanographic variables comprising the ocean/climate indices corresponds to a small number of apparent state shifts, so the data times series are too short for statistical discrimination between models of discrete multivariate states and models of continuous serially correlated variation in many variables, with the variation in many of the variables being mutually independent (Rudnick and Davis, 2003).

Tree ring data during the period of time with concurrent oceanographic measurements show a correlation with the ocean/climate indices, allowing statistical estimation of ocean/climate indices over the much longer period covered by tree ring data prior to the period of oceanographic measurements (Stahle et al. 1998; Biondi et al. 2001; D'Arrigo et al. 2001). At a much lower level of temporal resolution, there is some indication of the past relative sizes of salmon populations from evidence of their effect in transporting marine derived nutrients (Finney et al. 2000; Drake et al. 2002).

Here, we analyze some time series properties of a 331 year history of reconstructed annual Pacific Decadal Oscillation (PDO) estimates calculated from tree ring data by Biondi, Gershunov and Cayan (2001), available from

www.ncdc.noaa.gov/paleo/pubs/biondi2001/biondi2001.html.

The PDO estimates are graphed in Figure (1). A first order autoregressive model was fit to these data with a Bayesian analysis using uninformatively broad uniform priors for the three model parameters, the lag-1 serial correlation, the process mean, and the process standard deviation. The data are sufficient to determine these parameters quite well. Figure (2) shows the marginal posterior distribution for the lag-1 serial, correlation. Figure (3) shows the marginal posterior distribution for the process mean. Figure (4) shows the marginal posterior distribution for the process standard deviation.

A stochastic simulation using a first order autoregressive model, with parameter values corresponding to the posterior marginal means from the estimation, gives rise to time series realizations that look reasonably similar to the original estimates in their distribution of variation, and short to medium term pattern, but the simulations appear to under-represent the frequency of occasional long-duration excursions). One such realization is shown in Figure (5). This model, therefore, is a reasonable choice for simulating time series of random environmental variation in the operating model for a management strategy evaluation. For the same reason, this autocorrelation should be looked for in time series of recruits per spawner data or time series of residuals from stock-recruit regressions.

3. STOCK-RECRUIT MODELS

3.1. Elementary Density Dependence Mechanisms

Assume a habitat that provides a constant resource supply flux F . Assume a species where each individual exerts a constant per capita resource demand m just for biological maintenance. Finally, assume that per capita instantaneous population growth rate is proportional to the surplus of resource supply over aggregate demand. Thus

$$\begin{aligned} \frac{1}{N} \frac{dN}{dt} &= c(F - mN) \\ &= (cF) - (cm)N \\ &= a - bN \quad , \end{aligned} \tag{1}$$

where N is the current population size, and the proportionality constant c is a biological property of the species, and a and b simply collect terms for a more compact phenomenological notation.

The per capita demand term m is a biological property of the species. The resource supply term F is a property of the environment. So the phenomenological parameter b is a biological “constant” of the species, whereas a , since it is a product involving F , depends on the environment as well as on the species constant.

Integrating this differential equation gives

$$\begin{aligned} N_t &= \frac{N_0 e^{at}}{1 + N_0 (e^{at} - 1) \left(\frac{b}{a}\right)} \\ &= \frac{\alpha N_0}{1 + \beta N_0} \quad , \end{aligned} \tag{2}$$

for

$$\begin{aligned} \alpha &= e^{at} \\ &= e^{cFt} \quad , \end{aligned} \tag{3}$$

and

$$\begin{aligned} \beta &= (e^{at} - 1) \left(\frac{b}{a}\right) \\ &= (e^{cFt} - 1) \left(\frac{m}{F}\right) \quad . \end{aligned}$$

We note that this has the same form as the discrete time Beverton-Holt stock-recruit model, taking t to be the duration of a generation.

Recall that c and m are species specific biological constants, whereas F depends on the rate of supply of resources from the environment. Therefore, the magnitude of the α parameter will vary exponentially with environmental variation in the resource supply. A first order Taylor approximation of $(e^{cFt} - 1)$ as a function of c for small values of c yields cFt , so

$$\beta \simeq ctm \quad , \tag{5}$$

and, therefore, the variation in β with environmental variation in the resource supply will be comparatively slight.

If a factor extraneous to the resource supply causes density independent variation in mortality, this will appear as a multiplicative variation in N_{t+1} for the same N_t , so it too will appear effectively as variation in α , not β .

3.2. Beverton-Holt Stock-Recruit Model

The Beverton-Holt model (Beverton and Holt, 1957) is of the form

$$R = \frac{\alpha S}{1 + \beta S} \quad , \quad (6)$$

where S is the number of spawners giving rise to a particular brood, R is the number of resulting recruits corrected for harvest removals, α is the productivity parameter, and β is the density dependence parameter.

The Beverton-Holt model has the form of a standard mathematical saturation function (as appears, for example, in Michaelis-Menton chemical kinetics). That is, with this model, the recruitment rises monotonically with spawning escapement, asymptotically approaching a ceiling given by the ratio α/β . In other words, with the Beverton-Holt model, the penalty for greatly exceeding optimal escapement is a reduced efficiency in the marginal returns of recruits per spawner, but it does not cause an actual net depression in the number of recruits.

The Beverton-Holt model is frequently used in theoretical analyses. It is not the most popular model for fitting to actual data. In part this is probably a matter of convenience rather than poor fit, since doing the fitting properly requires more sophisticated statistical methods than does the popular alternative.

The Beverton-Holt model can be transformed to a linear relationship as

$$\left(\frac{S}{R}\right) = S \left(\frac{\beta}{\alpha}\right) + \left(\frac{1}{\alpha}\right) \quad , \quad (7)$$

so a traditional linear regression will reveal an estimate of α from the reciprocal of the y-intercept and then an estimate of β can be back-calculated from the slope which is the ratio of β to α . The serious shortcoming of this approach is that the assumption of normal error in the transformed space does not correspond to any reasonable error model for the process, so with real data the estimates will be biased and the calculated confidence limits will not be meaningful.

Proper fitting requires a non-linear regression, and generally it is assumed that the error, in the original space is multiplicative log-normal. Such an error structure could arise under the elementary model from normal variation in F or from log-normal variation in the density independent mortality.

Another feature of the statistical performance of the Beverton-Holt model that some practitioners might find repellent is the propensity to give unstable and biologically unreasonable estimates of the α parameter with weak data sets.

We will not necessarily take this to be a fault—it may be a correct representation of the weakness of the data set.

3.3. Ricker Stock-Recruit Model

The Ricker model (Ricker, 1954) is of the form

$$R = \alpha S e^{-\beta S} \quad , \quad (8)$$

where all the terms play the same role as in the Beverton-Holt, but the function has a fundamentally different shape at escapement levels where density dependence has strong influence. In contrast to the Beverton-Holt model, the Ricker model has a potential for literal “over-escapement.”

With the Ricker curve, as the spawning escapement increases beyond a particular level, $1/\beta$, the number of recruits declines, asymptotically approaching zero. The declining arm of the Ricker curve results from the model incorporating a more intensely operating density-dependence mechanism than that of the Beverton-Holt model, such that the intra-specific competition takes a heavier toll on population growth, as might occur when over population causes damage to the resource supply, or when the scramble for scarce resource forces all individuals into starvation rather than sorting individuals into winners and losers. The steepest slope on the ascending arm of the Ricker curve occurs at the origin, where the slope is simply α . The steepest portion of the descending arm occurs at escapement equal $2/\beta$, where the slope is $-\alpha e^{-2}$. Thus, the slope of the descending arm of the Ricker curve is always a constant fraction of the slope of the ascending arm.

The unharvested equilibrium escapement is $\ln \alpha / \beta$.

The Ricker is the most commonly used stock-recruit model for salmon data. It is most often fit by linear regression in the log space

$$\begin{aligned} \frac{R}{S} &= \alpha e^{-\beta S} \\ \ln(R/S) &= \ln \alpha - \beta S \quad . \end{aligned} \quad (9)$$

So, then, the y-intercept of the fitted regression line serves as an estimate of the natural log of the Ricker α , and the slope serves as an estimate of the negative of the Ricker β . Implicitly, the linear regression assumes that the error structure is additive normal in the log space, and therefore is multiplicative lognormal on R (Peterman, 1981). This representation of the process variation is reasonable

and consistent with natural mechanisms. Survival operates multiplicatively in its effect on recruitment, and the outcomes of multiple independent random processes interacting multiplicatively tend to log-normal distributions.

Formally, the log regression is

$$\begin{aligned} R &= \alpha S e^{-\beta S} e^\varepsilon \\ \frac{R}{S} &= \alpha e^{-\beta S + \varepsilon} \\ \ln(R/S) &= \ln \alpha - \beta S + \varepsilon \quad , \end{aligned} \tag{10}$$

where ε is normally distributed. Then conventionally, ε would be the normal residual from the regression.

Letting

$$\delta = e^\varepsilon \quad , \tag{11}$$

so that δ is lognormal, applied multiplicatively to represent the variation around the underlying expectation of the stock-recruit relationship, we note that this may be absorbed into variation in the Ricker α

$$R = (\alpha\delta) S e^{-\beta S} \quad . \tag{12}$$

This interpretation, that climatically driven environmental variation operates primarily through the density-independent productivity term of the model, rather than through the density dependent term, is consistent both with the elementary theoretical derivation of density dependent population growth models and with what we know about the mechanisms of density dependence in salmon and the effects of environmental variation on salmon population dynamics. Observed stock-recruit data sets, when fit with a stock-recruit curve, tend to give rise to residuals that do appear normally distributed in the log space, though often the residuals appear not to be independent, and instead exhibit temporal pattern.

The Ricker curve is not prone to giving superficially unreasonable point estimates when fit to weak data sets using simple statistical methods—this curve “likes” to conform to real data scatters showing little overt slope. However, this apparent “good” behavior can be misleading (Polacheck, Hilborn, and Punt, 1993). It is known that the point estimates of Ricker curves fit to truncated data sets with higher escapements culled, to mimic a data set restricted to the record under high harvest, are liable to give spuriously low estimates of the unharvested

equilibrium (S_k) and MSY escapement (S_{msy}), as the point estimates “follow” the depressed population downward. For this reason, an explicit representation of the correctly quantified parameter uncertainty is crucial.

3.4. Consequences of the Difference between Models

The difference in behavior between the two stock-recruit models can have profound implications for a management strategy evaluation. For example, in population viability analyses (PVA) using the Ricker model, it is often observed that modeled extinctions frequently follow directly after high population levels that caused density dependent population crashes. This will not occur with a Beverton-Holt PVA model.

For another example, the theoretical analysis by Walters and Parma (1996), arguing that a fixed harvest rate policy (rather than fixed escapement or fixed quota policy) is likely to confer good performance, used the Beverton-Holt model, where the resulting low harvests during periods of low population size allow a probability for population levels to build up in advance of periods of favorable environmental conditions during which the harvest policy can capitalize on the higher productivity. A Ricker model may not allow “stockpiling” population in this way (or at least to this extent) because of the cost of over-escapement. Thus, the stakes may be high for determining whether the Ricker or Beverton-Holt model applies.

Figure (6) shows a management strategy evaluation of constant escapement goal policies applied to Ricker and Beverton-Holt operating models that were fit to the *same* real data. The data series consists of brood tables for the Snake River (Columbia Basin) fall chinook (Table 4, p 38 of Langness and Reidinger, 2003).

Both stock-recruit curves give good fits to these data. The operating model assumes that the underlying geometric mean stock-recruit relationship is given by the curve fitted to the data, and the process variation is lognormal multiplicative with a log-space mean of zero and a log-space variance as given by the fit to the data, and a serial correlation as estimated from the 1-st order autoregressive fit to the tree-ring PDO reconstruction. The evaluation reports, on the y-axis of Figure (6), the long-term mean harvest that results from constant escapement policies with the magnitude of the escapement goal given by the x-axis. The S_{msy} for each respective stock-recruit curve, with its associated harvest (which is the performance that would be realized from an S_{msy} escapement in the absence of environmental variation, is located on the plot as a cross. We see that the MSY

escapement for the Beverton-Holt model is more than twice that for the Ricker model. We see from the location of the peaks of the performance curves that the optimal escapement goal to maximize long-term mean yield for the Beverton-Holt model is more than twice that of the Ricker model. Finally, we see that the system is much more forgiving of miscalibration of the escapement goal for the Beverton-Holt model, compared to the Ricker, as the former has a much broader and flatter peak to the performance curve.

3.5. Discriminating between the Models with Real Data

Both the Ricker and Beverton-Holt models may be derived mathematically from plausible mechanisms. Discriminating among them with available data sets may be quite difficult. Both models give rise to similar shapes for the ascending arm of the stock-recruit curve. If the data are from a heavily harvested stock, only the ascending arm will be represented in the data. For example, Figure (7) shows the Beverton-Holt and Ricker curves fit to the Snake River fall chinook data that were the basis for the preceding management strategy evaluation. In terms simply of statistical “fit,” there is little to choose between the two models.

Walters, LeBlond and Riddell (2004) reviewed the evidence pertaining to over-escapement in a suite of Fraser River salmon stocks for which there are long term data sets of high quality. These were 21 sockeye stocks and 2 pink salmon stocks, so the life histories in question were quite different from the chum stocks which are our concern. From inspection of the empirical stock-recruit patterns, the authors concluded that the data showed no evidence of over-escapement, in the sense of high spawning escapements being associated with disproportionately low consequent recruitment. In fact, scatter plots of $\ln(R/S)$ against S for these data sets show reasonable fits to a linear relationship, consistent with a Ricker model subject to multiplicative process variation. But all the data sets show essentially all of the data points lying to the left of the escapement level corresponding to $\ln(R/S) = 0$. In other words, these data sets from harvested stocks fail to explore the dynamics resulting from escapements greater than the unharvested equilibrium, so the data do not fall in the range where over-escapement could be manifested, and they do not fall in the range where Ricker versus Beverton-Holt dynamics can be distinguished among the process noise by simple graphical inspection.

3.6. Schnute-Kronlund model

In fact, stating the problem as a *statistical choice* between the Ricker and Beverton-Holt models is an oversimplification. If both models are plausible, differing only quantitatively in the intensity of the operation of density dependence, intermediates should also be plausible. The model of Schnute and Kronlund (1996) includes both the Ricker and Beverton-Holt models as special cases, as well as a spectrum of intermediates, essentially by decoupling the slope of the descending arm of the curve from the slope of the ascending arm. This allows, therefore, for realistic treatment of the uncertainty about the force of "over-escapement" in possibly depressing runs of these stocks.

The Schnute-Kronlund model is of the form

$$R = \frac{\alpha S}{(1 + \gamma \beta S)^{1/\gamma}} \quad , \quad (13)$$

where all the common terms play the same role as in the Ricker and the Beverton-Holt, and the γ parameter controls the family of shapes ranging from Ricker, when $\gamma = 0$, to Beverton-Holt, when $\gamma = 1$. At intermediate values of γ the shapes are intermediate. Figure (8) shows illustrations of a family of Schnute-Kronlund curves with a common α , with β adjusted to yield a common unharvested equilibrium " K ," and γ explored at intervals of one tenth. The MSY point for each curve is shown as a solid dot.

Thus, a statistically rigorous test for evidence for over-escapement could be conducted on the basis of the value of γ when fitting a Schnute-Kronlund model. Figure (9) shows the result of such an analysis for the Snake River fall chinook example. We see from the breadth of the posterior distribution that no value of γ in the range between 0 and 1 can really be ruled out, but there is a definite inclination in the direction of Beverton-Holt-like in preference to Ricker-like shapes since the probabilities are larger for γ closer to 1.

As with the Beverton-Holt and the Ricker models, environmental variation is expected to be manifest almost exclusively in the α parameter, of the Schnute-Kronlund model, and the presumption is that this will appear more or less as multiplicative log-normal deviations. Given the presence of one more parameter, γ , and given that the Schnute-Kronlund model can reduce to a Beverton-Holt, it will fall prey to the same potential for biologically unreasonable parameter values with weak data sets. This argues for the importance of Bayesian methods for full representation of the uncertainty in all parameters, and also incorporating biological constraints in the prior distributions.

It is worth pointing out that environmentally driven variation in the density independent productivity parameter α will still affect the realized “carrying capacity” and MSY escapement. The solution for carrying capacity, S_k , the unharvested equilibrium, is

$$S_k = \frac{\alpha^\gamma - 1}{\gamma\beta} \quad . \quad (14)$$

The MSY escapement is found from the condition for the first derivative of harvest, H , with respect to S , being equal 0,

$$\frac{(1 + \gamma\beta S_{msy})^{\frac{1}{\gamma}}}{\alpha} + \frac{\beta S_{msy}}{1 + \gamma\beta S_{msy}} - 1 = 0 \quad , \quad (15)$$

which requires numerical solution to find the root. The associated harvest is

$$H_{msy} = \frac{\beta S_{msy}^2}{1 + \beta S_{msy}} \quad . \quad (16)$$

Figure (10) shows S_k as a function of α for a family of Schnute-Kronlund curves with a series of γ values, where for each γ the value of β was set to give $S_k = 1000$ at $\alpha = 4$. Figure (11) shows S_{msy} as a function of α for the same family of Schnute-Kronlund curves.

4. ANALYSES OF THE AYK CHUM STOCKS

The analyses reported here used Bayesian inference, and, except where noted explicitly, the prior distributions were uninformatively broad independent uniforms. The likelihood functions used the assumed underlying deterministic stock-recruit model with multiplicative log-normal environmental variation, treating the standard deviation of that environmental variation as a parameter to be estimated jointly with the parameters of the stock-recruit model. The data were accepted at face value, and possible measurement error was ignored.

4.1. Andreafsky Summer Chum

A previous analysis of the stock-recruit data for the Andreafsky River Chum is given in Clark (2001a). The data used in the present analysis were from the column labelled “Tracy” in an Excel spread sheet supplied by Tracy Lingnau, in January 2004. The values in these brood tables were considerably different from

those reported by Clark (2001a). The present analysis does not inquire into the differences. The brood tables used here report spawners and total recruits for brood years 1972 through 1995.

Figure (12) shows a scatter plot of the stock and recruitment pairs, labelled by brood year and with points connected in chronological sequence. The data scatter is superimposed on the Ricker curve formed from the posterior marginal modes of estimates of the Ricker α and β . The scatter is considerable, and the data cloud shows little shape or pattern in the original space. Nevertheless, the Ricker model gives an unambiguous fit, as shown by the posterior marginal for α in Figure (13), the posterior marginal for β in Figure (14), and the posterior marginal for σ_ε , the standard deviation of the log of the multiplicative process variation, in Figure (15).

However, a plot of the log-space residuals from the Ricker fit, namely ε the log of the process variation, by brood, in Figure (16) puts matters in a different light. We see a very marked downward trend that is essentially linear. Biologically this tells us that the Andreafsky chum stock has been experiencing a fairly continuous downward trend in productivity over the 24 year period of record. This definitely should motivate inquiry into *why* the productivity is declining, or at least into what other variables, including the productivity of other stocks, may be correlated with it.

Mathematically, this tells us that the distribution of the variation that we are attributing to ε is non-stationary, and in fact highly patterned and partially predictable as a fairly consistent time trend. Therefore, for purposes of short term prediction, our fitting method, which incorrectly assumes that the annual departures are independent, inflates the estimate of the process variation, σ_ε , and inflates the apparent uncertainty of the estimates of the underlying Ricker parameters, and biases the estimates of the Ricker parameters toward a compromise mean for the data series, whereas more accurate year-specific estimates of the stock-recruitment relation could be obtained from a model that incorporated the observed time trend in α that was revealed by the residuals. Such modeling should be a priority.

Continuing, for the time being, with the analysis of the Ricker fit assuming independent process variation, the Bayesian approach allows calculation of explicit posterior distributions for quantities that depend on the estimated parameters, based on the *joint* posterior distribution of those parameters. Figure (17) shows the posterior distribution for the spawning escapement at the unfished equilibrium, S_k , for the underlying Ricker parameters. Figure (18) shows the posterior

distribution for the MSY spawning escapement, S_{msy} , for the underlying Ricker parameters. Figure (19) shows the posterior distribution for the MSY harvest rate (proportion of the recruits), F_{msy} , for the underlying Ricker parameters.

The “modal Ricker curve” plotted in the figures is constructed from the posterior marginal modes of the two Ricker parameters. While this plotted curve provides a clear visual reference, it fails to do justice to the inference at several levels. First of all, the joint mode may not correspond to the respective marginal modes. Second, the inference quantifies uncertainty that ideally should be represented in the graphical portrayal (and taken into account when the inference is used for management decisions). The Bayesian inference procedure allows for calculation of posterior distributions of any function of the parameters. In Figure (20), the posterior distributions of recruitment itself is shown by way of its mode (shown as a solid square), and its 95% posterior interval (defined by the two 2.5% tails of the posterior distribution), at three selected values for spawning escapement—the values for S_{msy} , S_k , and twice S_k calculated from the modal Ricker. The spread of uncertainty, owing to parameter uncertainty, is striking. The spread at larger escapements is very large, even with the model confined to the Ricker form.

The preceding figure reflects only the parameter uncertainty in the Ricker curve applying to the Andreafsky chum data. For any given brood (year), the process variation contributes further uncertainty. With process variation operating multiplicatively on the Ricker α , we may, during the course of inference, sample the inferred process variation as well, to obtain a posterior distribution that reflects the cumulative effects of parameter uncertainty coupled with the process variation. Figure (21) shows such a distribution for the MSY spawning escapement for any single brood. Comparing Figure (21) with Figure (18) shows how the addition of the process variation increases the uncertainty over parameter uncertainty alone.

The stock-recruit data cloud for the Andreafsky shows insufficient shape to reasonably constrain a Beverton-Holt fit, so the results of an attempt at Bayesian estimation will be strongly influenced by the prior, and results of use of a uniform prior will be influenced by the choice of parametrization. To illustrate a “natural” parametrization, with ready interpretability even for a very broad range of values, consider defining the Beverton-Holt in terms of θ , the *angle* of the slope at the origin, and R_{sat} , the saturation recruitment

$$\theta = \text{Tan}^{-1}(\alpha) \quad , \quad (17)$$

and

$$R_{sat} = \frac{\alpha}{\beta} \quad . \quad (18)$$

Then, the Beverton-Holt relationship becomes

$$R = \frac{Tan(\theta)R_{sat}S}{R_{sat} + Tan(\theta)S} \quad . \quad (19)$$

This parametrization allows for a graceful uniform prior on the angle over the entire logical range between 0 and 90 degrees. It allows for a uniform prior on the saturation level that provides equal probabilities at high levels up to an interpretable explicit limit.

With this parametrization, a uniform prior on θ between 0 and 90, and a uniform prior on R_{sat} between 0 and 2.5 million, the posterior marginals on these two parameters are as shown as in Figures (22) and (23). Even though the ceiling of 2.5 million recruits is more than 4 times the largest recruitment observed in the data, and more than 6 times the apparent mode for the ceiling, this limit is not high enough to contain the range of values consistent with the likelihood: the high tail of the posterior distribution does not taper to zero in this range. Raising the upper limit for the uniform prior on R_{sat} extends the tail on the posterior, still without causing it to taper appreciably, and changes the shape of the posterior marginal for θ , shifting to a lower mode that is just detectable as a slight shoulder in Figure (22). This poorly defined inference reflects the insufficiency of the data for determining a fit to the Beverton-Holt model.

With the Beverton-Holt fit undetermined, the Schnute-Kronlund model will not yield a clear inference either. In order to pursue the question of quantitative evidence for the potential for “over-escapement,” the posterior distribution for the Ricker parameter α was used as a prior for α in a Bayesian inference on the Schnute-Kronlund model, with uninformatively broad uniform priors on β , γ , and σ_ε . This constraint on α , favoring a fit to the Ricker, was sufficient for the inference to yield an unambiguous joint posterior. The results are shown for the posterior marginal on β in Figure (24), S_{msy} in Figure (25), and γ in Figure (26). Notwithstanding the prior favoring a fit to the Ricker, and therefore a low value for γ , the posterior marginal shown in Figure (26) indicates more evidence for higher values of γ and therefore more tendency toward Beverton-Holt-like shapes.

The effect of parameter uncertainty, in the Schnute-Kronlund fit with the constrained prior on α , on the uncertainty in the recruitment at selected levels of

spawning escapement is shown in Figure (27). To facilitate comparison with the same uncertainty quantification for the Ricker model, shown in Figure (20), the selected escapements are the values for S_{msy} , S_k , and twice S_k calculated from the modal Ricker. The spread of uncertainty, owing to parameter uncertainty, at larger escapements is not as large as in the Ricker analysis, and the posterior envelope is more level, as expected from the tendency to a Beverton-Holt shape.

4.2. Anvik Summer Chum

A previous analysis of the stock-recruit data for the Anvik River Chum is given in Clark and Sandone (2001). The data used in the present analysis were supplied by Tracy Lingnau, ADFG, as an Excel spreadsheet, received in January 2004. The values in these brood tables were similar, but not identical, to those reported by Clark and Sandone (2001) as their “mixed stock fishery model two,” which, however, stopped with 1993. The present analysis does not inquire into the differences in the data. The brood tables used here report spawners and total recruits for brood years 1972 through 1997.

Figure (28) shows a scatter plot of the stock and recruitment pairs, labelled by brood year and with points connected in chronological sequence. The data scatter is superimposed on the Ricker curve formed from the posterior marginal modes of estimates of the Ricker α and β . The scatter is considerable, and the data cloud shows little shape or pattern in the original space. Nevertheless, the Ricker model gives an unambiguous fit, as shown by the posterior marginal for α in Figure (29), the posterior marginal for β in Figure (30), and the posterior marginal for σ_ε , the standard deviation of the log of the multiplicative process variation, in Figure (31).

A plot of the log-space residuals from the Ricker fit, namely ε the log of the process variation, by brood, in Figure (32) shows a marked increasing trend from 1972 to 1982, and a consistent downward trend from 1982 to 1997. So, for this stock, too, the distribution of the variation that we are attributing to ε is non-stationary and highly patterned.

4.3. Kwiniuk Chum

A previous analysis of the stock-recruit data for the Kwiniuk River Chum is given in Clark (2001b). The data used in the present analysis were from table 9 of that document. The brood tables used here report spawners and total recruits for brood years 1965 through 1995.

Figure (33) shows a scatter plot of the stock and recruitment pairs, labelled by brood year and with points connected in chronological sequence. The data scatter is superimposed on the Ricker curve formed from the posterior marginal modes of estimates of the Ricker α and β . The scatter is considerable, and the data cloud shows little shape or pattern in the original space. Nevertheless, the Ricker model gives an unambiguous fit, as shown by the posterior marginal for α in Figure (34), the posterior marginal for β in Figure (35), and the posterior marginal for σ_ε , the standard deviation of the log of the multiplicative process variation, in Figure (36).

A plot of the log-space residuals from the Ricker fit, namely ε the log of the process variation, by brood, in Figure (37) shows an irregular downward trend, or perhaps a simple shift from a high set of values to a low set of values in 1980. In an attempt to explore the implications of the latter possibility, separate Ricker curves were fit independently to the data from 1965-1979 and 1980-1995. The resulting Ricker curves are distinct, as shown in Figure (38). The productivity during the earlier period was more than twice that of the more recent period, as shown by the posterior marginals on the Ricker α in Figure (39). The Ricker β , however, was quite similar in the two periods, as shown in Figure (40), consistent with our theoretical expectation that the predominant effect of environmental change should be on the α parameter.

5. SYNTHESIS

There is no evidence for over-escapement in any of the three AYK chum stocks with long enough data series to support a stock-recruit analysis. All three stocks show large recent declines in productivity. Figure (41) overlays the three respective time series of the log-space residuals from the Ricker fit, by brood. The overlay reveals that all three exhibit the same, nearly linear, downward trend, in the recent two decades, and all three conform to an early episode of increasing trend. Figure (42) shows linear and quadratic fits to the aggregate of the three respective time series. The linear fit achieves an R^2 of 0.20, and the quadratic fit achieves an R^2 of 0.28. This is to say that about one quarter of the variation observed on a three decade time scale can be accounted for (and predicted) as low frequency trend.

Visual assessment of Figure (41) suggests that there is also a degree of agreement in the short term excursions from that trend. To appraise this quantitatively, residuals from the common linear and quadratic trends were computed for the re-

spective stock specific time series. The correlations between the detrended time series of the three stocks were computed, and submitted to principal component decomposition.

The principal components after linear detrending are

| | PCA I | PCA II | PCA III |
|----------------------|--------|--------|---------|
| Eigenvalue | 1.743 | 0.688 | 0.569 |
| Eigenvector elements | | | |
| Andreafsky | 0.554 | 0.572 | 0.605 |
| Anvik | -0.772 | 0.625 | 0.115 |
| Kwiniuk | -0.312 | -0.531 | 0.788 |

For the linear detrending, the first principal component accounted for 58% of the variance (after detrending, which itself accounted for 20% of the original variance), and the associated eigenvector was essentially a simple sum of the three stocks. This confirms that the dominant mode of variation, even at the shorter time scales, has the three stocks responding in concert.

The principal components after quadratic detrending are

| | PCA I | PCA II | PCA III |
|----------------------|--------|--------|---------|
| Eigenvalue | 1.634 | 0.754 | 0.611 |
| Eigenvector elements | | | |
| Andreafsky | 0.548 | 0.555 | 0.616 |
| Anvik | -0.753 | 0.655 | 0.069 |
| Kwiniuk | -0.364 | -0.501 | 0.785 |

For the quadratic detrending, the first principal component accounted for 54% of the variance (after detrending, which itself accounted for 28% of the original variance), and the associated eigenvector was essentially a simple sum of the three stocks. This again confirms that the dominant mode of variation, even at the shorter time scales, has the three stocks responding in concert.

All three stocks show large uncertainty in the parameters of the stock recruitment curve, resulting in large uncertainty in the S_{msy} . The uncertainty in the S_{msy} associated with the underlying mean stock-recruit relationship spans roughly a two-fold range. The uncertainty in the S_{msy} from one brood to the next, thus taking account of process variation as well as parameter uncertainty, is much larger.

In the absence of evidence for overescapement, there is merit to considering a

management strategy of *not* decreasing the escapement goal to track the trend of decreasing productivity of these stocks. This strategy will position the stocks to capitalize on higher productivity events when they occur. Some high productivity events can arise from the high frequency variation, even in the time before the long term trend turns around.

The between-stock temporal correlation in the variation in productivity, both on short and long time scales, lends credence to the information content of the stock-recruit brood tables. (Random measurement error variation will not exhibit correlation between stocks.) The correlation shows there is promise in a search for specific environmental variables that are the drivers, to elucidate the causes of the ongoing decline and episodic deviations. The fact of the correlation indicates that the cause almost certainly includes one or more common factors operating on a regional scale—this could be a meteorological factor affecting the freshwater phase of the life history, an oceanographic factor affecting the saltwater phase, or competition in saltwater, or variation in ocean harvest mortality that is not accounted for in the run reconstructions.

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