Model complexity and catch-age analysis

Laura J. Richards and Jon T. Schnute

Abstract: Catch-age analysis has become a standard tool of fisheries stock assessment. Modern catch-age models can contain dozens or even hundreds of parameters to be estimated. In this paper, we compare the performance of a typically complex catch-age model with a simpler model in which the population age structure is represented only by the annual mean age. We find that the population trajectory estimated from the simple model is in general agreement with the trajectory from the catch-age analysis. We suggest that the simple model can serve as both an intuitive and quantitative aid to interpreting results from the complex model. For example, the contrast between models highlights the role of technically complex assumptions. To some extent, errors in the age structure data cancel in calculating the mean age. Thus, our analysis suggests options available for investigating stocks where only summary age data are reliable.

Résumé : L'analyse de l'âge à la capture est devenue un outil courant pour évaluer les stocks de poissons d'importance commerciale. Mais les modèles modernes de l'âge à la capture peuvent contenir des dizaines, sinon des centaines, de paramètres à évaluer. On compare dans la présente étude la performance d'un modèle complexe typique et d'un modèle plus simple, où la structure d'âge de la population n'est représentée que par l'âge moyen annuel. Il apparaît que la trajectoire de la population estimée d'après le modèle simple concorde généralement avec la trajectoire obtenue par l'analyse de l'âge à la capture. Cela indique que le modèle simple peut servir d'aide quantitative et intuitive pour interpréter les résultats du modèle complexe. Par exemple, le contraste entre les modèles met en lumière le rôle des hypothèses techniquement complexes. Dans une certaine mesure, des erreurs dans les données sur la structure d'âge s'annulent dans le calcul de l'âge moyen. Notre analyse fait ressortir des options disponibles pour étudier des stocks lorsque seules les données sommaires sur l'âge sont fiables.

[Traduit par la Rédaction]

Introduction

Catch-age analysis has become a standard tool of modern fisheries stock assessment (Megrey 1989). The analysis attempts to reconstruct population numbers at age and time, based on fishery catch, sampled age proportions, and other ancillary data. Implementations range from deterministic back-calculations, such as sequential population analysis (Gulland 1965) and cohort analysis (Pope 1972), to the statistical models of Fournier and Archibald (1982), Deriso et al. (1985), and Methot (1989, 1990). More recent approaches consider both process and measurement errors (Pella 1993; Schnute 1994), either in a likelihood context (Sullivan 1992; Gudmundsson 1994; Schnute and Richards 1995) or in a Bayes context (McAllister et al. 1994; McAllister and Ianelli 1997; Punt and Hilborn 1997).

This paper articulates theoretical and practical differences between historical and modern analyses. In particular, we compare the performance of a typically complex catch-age model with a simpler model described by Schnute and Richards (1998) in which the population age structure is represented only by the mean annual age. Our simple model is based on moment equations similar to those found by Deriso (1980), Schnute (1985, 1987), and Fournier and Doonan

L.J. Richards[1] and J.T. Schnute. Department of Fisheries and Oceans, Science Branch, Pacific Region, Pacific Biological Station, Nanaimo, BC V9R 5K6, Canada.

[1] Author to whom all correspondence should be addressed. e-mail: richardsl@dfo-mpo.gc.ca

(1987), as reviewed by Hilborn and Walters (1992, chap. 9). In particular, we assume knife-edged recruitment to the fished population whereas catch-age analyses typically assume that recruitment occurs over a range of ages. Using data from a real population, we find that reconstructed population trajectories are remarkably similar for the simple and complex models. However, recruitment trends estimated by the simple model are somewhat smoother than those inferred from the complex model.

Simple models can serve as intuitive and quantitative aids to interpreting results from complex models. For example, analytical results from a simple model can guide the understanding of a complex model, where analytical results are not available. In addition, differences in numerical results highlight the role of technically complex assumptions.

Where possible, we choose previously published models and data to simplify our presentation. Our data set and complex model are described in Richards et al. (1997), where the model has been adapted from Schnute (1994) and Schnute and Richards (1995) to address specific features of the data. The data here, updated from Richards and Olsen (1996) and Richards et al. (1997), are selected from the fishery for Pacific ocean perch (*Sebastes alutus*) in southern Queen Charlotte Sound, British Columbia, Canada. Our simple model derives from moment equations discussed by Schnute and Richards (1998).
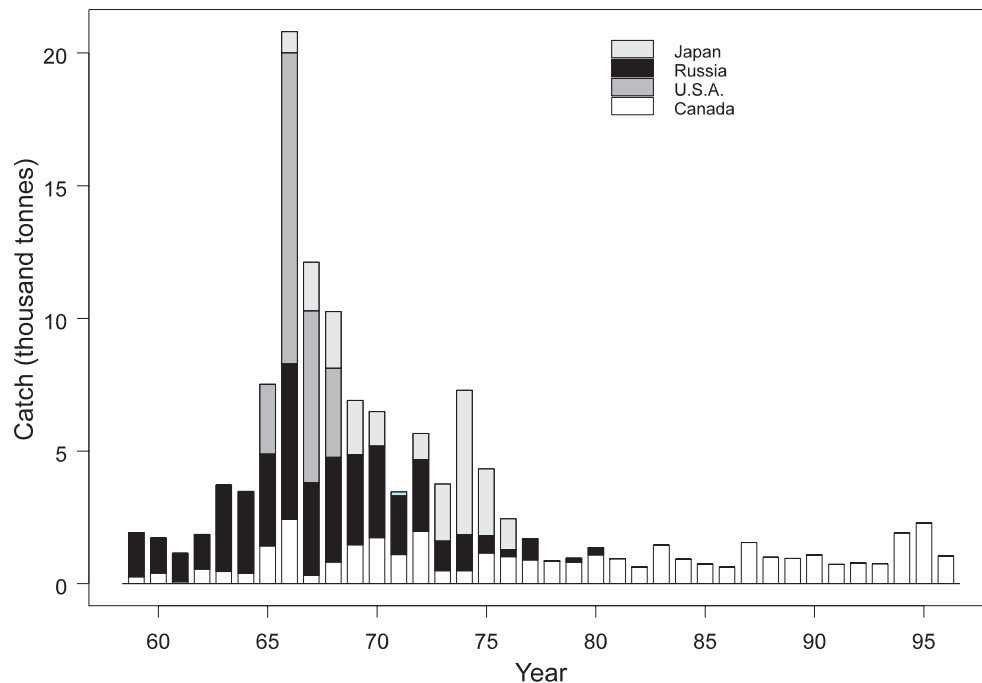
Section 1 describes the Pacific ocean perch data set and data preprocessing requirements. Our simple model is defined and tailored for the Pacific ocean perch data in Section 2, based on mathematical derivations in the Appendix. Results of the model comparison are presented in Section 3. We discuss further implications of our analysis in Section 4.

950

Can. J. Fish. Aquat. Sci. Vol. 55, 1998

Fig. 1. Pacific ocean perch trawl catch reported by nation from southern Queen Charlotte Sound, British Columbia, between 1959 and 1996.

1. Data

Fishery catch and proportions at age sampled from the catch constitute the core data for any catch-age analysis. We have updated these Pacific ocean perch data from Richards et al. (1997) to include information from the most recent year (1996). The catch data in Fig. 1 show that the stock was subjected to a large multinational fishery until the mid-1970s, followed by a comparatively small Canadian fishery. Large catches were harvested by Soviet and Japanese fleets during the late 1960s and early 1970s, prior to extended jurisdiction. Other rockfish (*Sebastes* spp.) stocks along the Pacific coast of North America were also targeted by Soviet and Japanese fleets at this time. Several studies in the early 1980s (Ketchen 1981; Kimura 1981; Archibald et al. 1983) indicated depletion of the Pacific ocean perch stock by the late 1970s. The subsequent Canadian fishery was therefore restricted by low annual quotas and other management measures.

Two different methods have been used to determine the Pacific ocean perch age proportions illustrated in Fig. 2. Between 1963 and 1976, ages were obtained from surface readings of otoliths (Archibald et al. 1983), a method known to underestimate true ages older than about 15–16 years (Stanley 1987). Between 1977 and 1996, ages were obtained by the break and burn method (Chilton and Beamish 1982). Actual break and burn ages range up to 79 years. However, ages 29 years and older are grouped in Fig. 2, consistent with the maximum observed surface ages. The two blank columns portray the absence of age data for 1986 and 1988.

In Fig. 2, the modal age-class within a year is always older than the age-class at first recruitment, indicating that availability to the fishery increases with age for younger ages. Our complex model for these data, as in most catch-age analyses, uses the complete age proportion data set and allows selectivity by the fishery to vary with age. However, our simple model

uses only the mean age and requires the assumption of knife-edged recruitment. We selected age 9 years as the age at recruitment for the simple model because strong year-classes often become apparent at age 9 years, particularly in 1970 and 1985.

We make two simplifications in the calculation of mean age, portrayed as the solid line in Fig. 2. First, to accommodate some of the uncertainty in true ages from surface readings, we assign an age of 29 years to all fish in the accumulator age-class. Second, we assign an age of 9 years to all fish younger than the age at recruitment. In this scenario, we assume that the small proportions at age 7–8 years actually represent fish of age 9 years that were incorrectly aged. Figure 2 provides some supporting evidence; the largest proportions at age 8 years occur in 1970, 1985, and 1989, years for which a large year-class has recruited at age 9 years. Such a pattern is suggestive of ageing error rather than consecutive strong year-classes. An alternative approach might be to exclude data on fish younger than age 9 years from both the total catch and the age proportion data. These procedures lead to similar results and we only report the ageing error scenario in the discussion below.

The trend in mean age in Fig. 2 contains interesting differences from the year-class trends. Mean age is essentially constant for the 1963–1976 period; the strong year-class appearing in 1970 acts to counterbalance the increasing age of earlier strong year-classes. Mean age increases between 1976 and 1983, and the subsequent decrease in mean age until 1987 coincides with the appearance of the next strong year-class. Obviously, the relatively large proportions in the accumulator age-class influence the mean age calculation.

Catch and age proportion data alone are generally inadequate to reconstruct the history of a fish population. Two series of research trawl surveys are also available to index Pacific ocean perch abundance (Fig. 3). The first series was conducted

Fig. 2. Pacific ocean perch age proportions sampled from the Canadian catch for recruited ages of 7 years and older and the mean age (solid line), computed as discussed in the text. The radius of a circle is proportional to the measured age proportion, where data are scaled to sum to 1 across each column and ages 29 years and older are grouped. The vertical dotted line distinguishes age data obtained by surface readings of otoliths (1963–1976) from later break and burn readings (1977–1995). No age proportion data are available for 1986 or 1988.
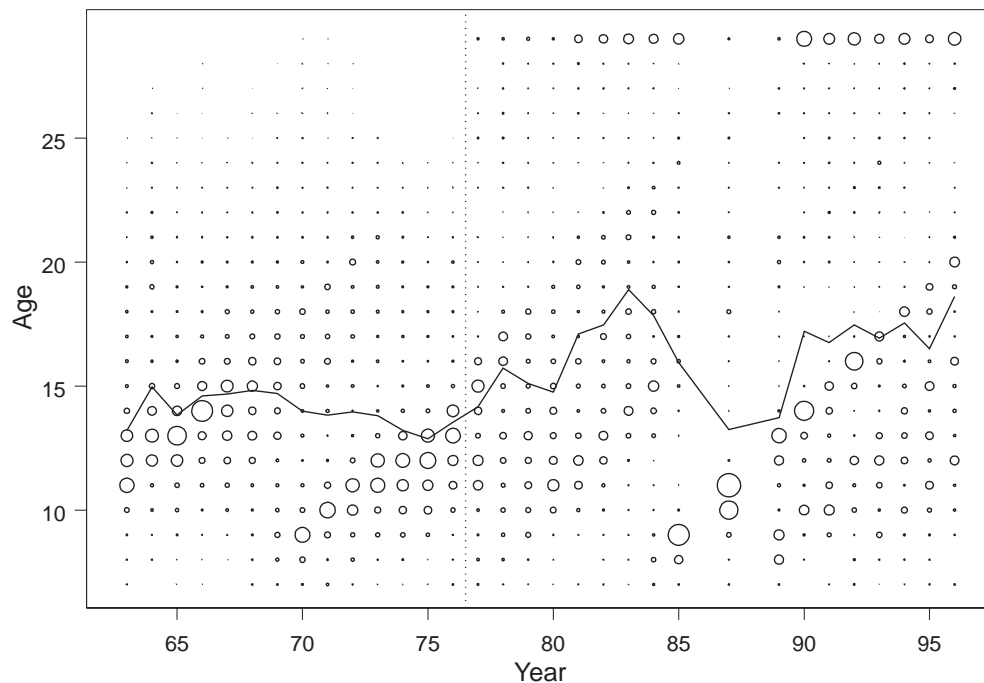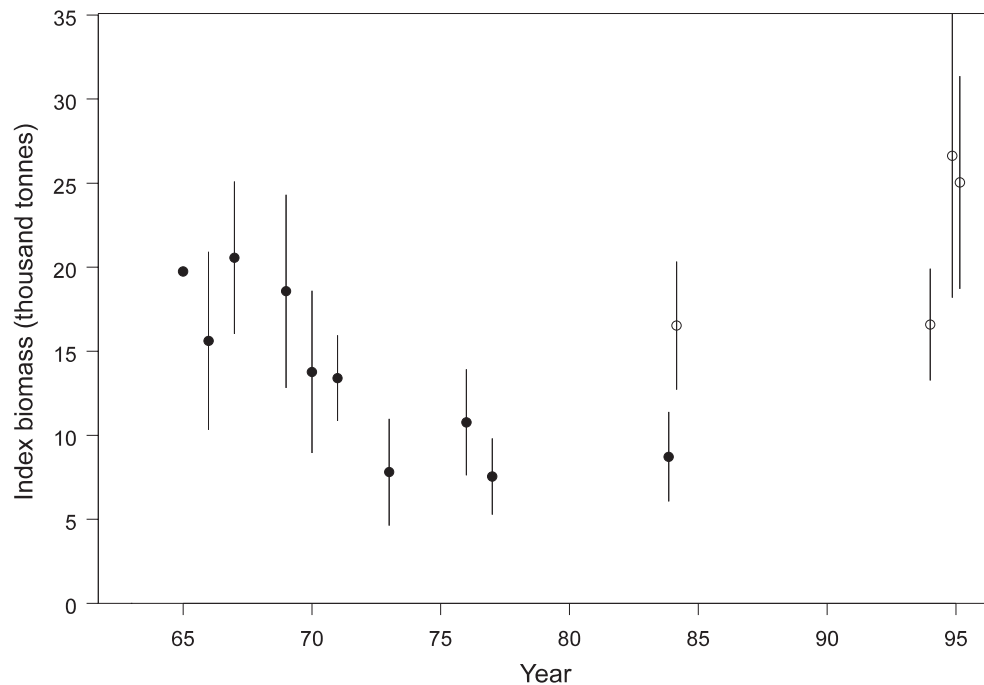

Fig. 3. Point estimates and 95% confidence intervals for the Pacific ocean perch trawl abundance indices obtained by swept-area trawl surveys using a research vessel (solid circles) and chartered commercial vessels (open circles).

by a research vessel between 1965 and 1984. The second series was conducted by a chartered commercial vessel, with a calibration survey in 1984 and subsequent surveys in 1994 and 1995 (Hand et al. 1995; Yamanaka et al. 1996). Confidence intervals in Fig. 3 are determined from standard application of sampling theory for a stratified random design (e.g., Cochran 1977, chap. 5). The confidence interval is missing for the first survey because only one sample tow was completed in one of the four survey depth strata for that year. At best, these intervals provide a minimal estimate of the true survey variance;

Table 1. Mean age model, assuming knife-edged recruitment.

Data

(T.1) $\quad x_t = \sum_a a p_{at}$

(T.2) $\quad w_t = \sum_a w_{at} p_{at}$

(T.3) $\quad D_t;\ C_t = D_t/w_t$

(T.4) $\quad (I_{it}, f_{it});\ t \in \mathbf{T}_i;\ i = 1, 2$

Parameters

(T.5) $\quad \Theta = (M, q_1, q_2, A_1, P_1, \{R_t\}_{t=1}^T, R, \gamma, \rho, \kappa, \tau_2)$

(T.6) $\quad \sigma^2 = \rho \kappa^2,\ \tau_1^2 = (1 - \rho)\,\kappa^2$

(T.7) $\quad \kappa^2 = \sigma^2 + \tau_1^2,\ \ \rho = \dfrac{\sigma^2}{\sigma^2 + \tau_1^2}$

Unobserved states

(T.8) $\quad R_t, S_t, P_t, B_t, A_t$

Initial states ($t = 1$)

(T.9) $\quad B_1 = w_1 P_1$

(T.10) $\quad S_1 = P_1 - C_1$

State dynamics ($2 \leq t \leq T$)

(T.11) $\quad R_t = R^{1-\gamma} R_{t-1}^{\gamma} e^{\sigma \delta_t}$

(T.12) $\quad P_t = R_t + e^{-M} S_{t-1}$

(T.13) $\quad B_t = w_t P_t$

(T.14) $\quad A_t = 1 + \dfrac{P_t - R_t}{P_t} A_{t-1}$

(T.15) $\quad S_t = P_t - C_t$

Observations

(T.16) $\quad I_{it} = [q_i (B_t - f_{it} D_t)] e^{\tau_1 \varepsilon_{it}};\ t \in \mathbf{T}_i;\ i = 1, 2$

(T.17) $\quad x_t = A_t e^{\tau_2 \eta_t};\ t \geq 1$

Likelihoods

(T.18) $\quad L_1(\mathbf{Q}) = \displaystyle\prod_{t=2}^{T}\left[\dfrac{1}{(2\pi)^{1/2}\sigma}\exp\left(-\dfrac{1}{2}\delta_t^2\right)\right]$

(T.19) $\quad L_2(\mathbf{Q}) = \displaystyle\prod_{i=1}^{2}\prod_{t\in \mathbf{T}_i}\left[\dfrac{1}{(2\pi)^{1/2}\tau_1}\exp\left(-\dfrac{1}{2}\varepsilon_{it}^2\right)\right]$

(T.20) $\quad L_3(\mathbf{Q}) = \displaystyle\prod_{t=1}^{T}\left[\dfrac{1}{(2\pi)^{1/2}\tau_2}\exp\left(-\dfrac{1}{2}\eta_t^2\right)\right]$

(T.21) $\quad L(\mathbf{Q}) = \displaystyle\prod_{i=1}^{3} L_i(\Theta)$

(T.22) $\quad \ell(\mathbf{Q}) = -2 \log L(\Theta) - K$

$\qquad\quad = (T-1)\log(\sigma^2) + (T_1 + T_2)\log(\tau_1^2) + T \log(\tau_2^2)$

$\qquad\quad + \displaystyle\sum_{t=2}^{T}\delta_t^2 + \sum_{i=1}^{2}\sum_{t\in \mathbf{T}_i}\varepsilon_{it}^2 + \sum_{t=1}^{T}\eta_t^2$

they incorporate only the variation in catch rates among survey tows within a given year.

2. Model development

The simple model is presented in Table 1, where the prefix "T" is used to distinguish tabulated equations from those in the text. Table 1 is divided into seven sections that describe the input

data, model parameters, unobserved states, initialization assumptions, state dynamics, observation equations, and corresponding likelihood functions. This framework follows the state space design principles described by Schnute (1994).

The data section must be tailored to represent each specific data set. For Pacific ocean perch, input data include the age proportions p_{at} and weights w_{at} for each age-class a and year t, the annual catch biomass D_t, the two abundance index survey series (I_{1t}, I_{2t}) available for sets of years ($\mathbf{T}_1$, $\mathbf{T}_2$), and the corresponding catch fractions (f_{1t}, f_{2t}) harvested prior to the survey during survey years. Age-classes $a = 1,...,21$ correspond to ages 9–29 years, where the raw data have been preprocessed as described in Section 1 and the last age-class acts as an accumulator. Years $t = 1,...,T$ correspond to the 1963–1996 period, so that $T = 34$.

Equations (T.1)–(T.2) define observations of the mean annual age-class x_t and fish weight w_t, respectively, where the age proportions are defined such that $\sum_a p_{at} = 1$ for each year t. Values of x_t differ by a constant 8 units from the mean age in Fig. 2 because of the conversion between age and age-class. The mean weights w_t play a minor role in the simple model, which is based primarily on fish numbers. However, values w_t are required to convert catch biomass D_t to catch numbers C_t in (T.3). Because age data are missing for 1986 and 1988, values w_t for those years are interpolated from adjacent years.

The state dynamics for the simple model are drawn primarily from Schnute and Richards (1998), who present deterministic models only. The stochastic assumptions in Table 1 closely parallel those in the complex model (Schnute and Richards 1995; Richards et al. 1997). We assume that process error σ in the recruitment complements measurement error τ_1 in the survey abundance index. Intuitively, apparent variations in abundance can be explained primarily though variability in recruitment (high process error σ) or indexing (high measurement error τ_1). Such ambiguities are inherent to most models that include both measurement and process error (Kendall and Stuart 1979, chap. 29). We resolve this ambiguity by fixing the variance ratio ρ between recruitment and total variance κ^2 through the relationships (T.6)–(T.7). A value of ρ near 1 corresponds to high variance in recruitment and low variance in the model fit to the survey index. Conversely, a low value of ρ corresponds to near constant recruitment and high variance in the survey index fit.

Our simple model includes five unobserved state variables (T.8) for each year t. Recruitment R_t occurs at the start of the year, resulting in the population P_t, biomass B_t, and mean age A_t. After the catch is removed, the survivors S_t remain at the end of the year and experience natural mortality M prior to the start of the following year. The model parameter vector Θ in (T.5) includes all recruitments R_t, plus the initial states P_1 and A_1. These give initial values for the remaining two states B_1 and S_1 in (T.9)–(T.10).

Because the unobserved state variables R_t are also treated as explicit parameters, they do not require an update equation. The model equation (T.11) serves only to identify the recruitment variance σ^2, rather than to describe a specific biological process. To allow possible recruitment correlation, we consider the lognormal autoregressive process

$$\log R_t = \log R + \gamma(\log R_{t-1} - \log R) + \sigma \delta_t$$

Fig. 4. Estimates and 95% confidence intervals from the simple and complex models for Pacific ocean perch exploitable biomass between 1963 and 1996.
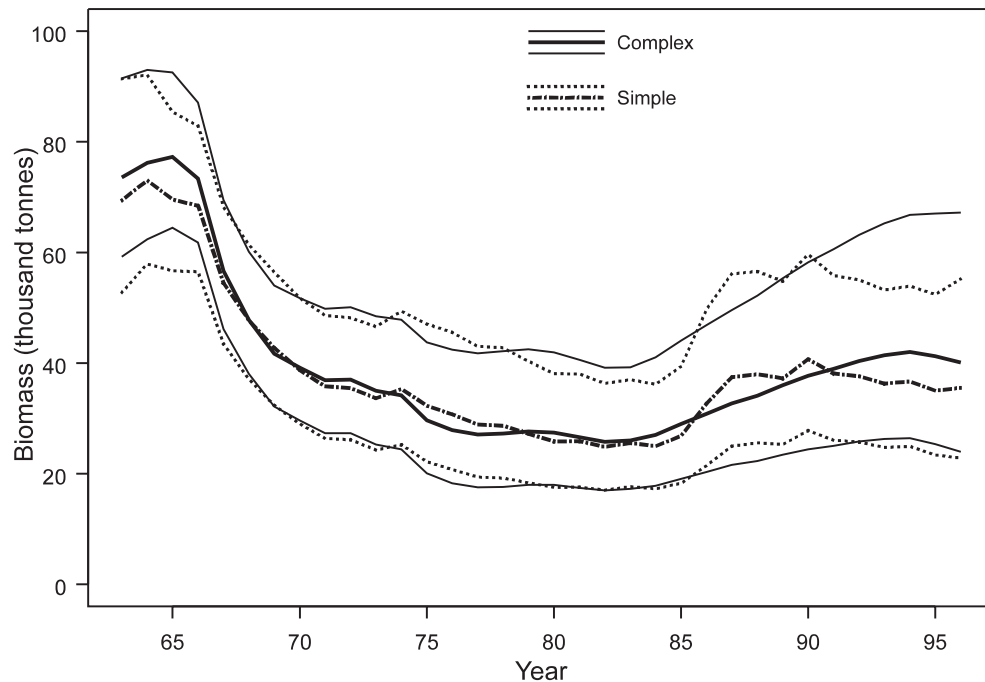
equivalent to (T.11), where the standard normal variates δ_t are assumed independent.

Equations (T.12)–(T.15) sequentially update the remaining four state variables (P_t, B_t, A_t, S_t) for $t = 2,...,T$. Thus, the population P_t in (T.12) at the beginning of year t consists of the recruits R_t and the survivors $e^{-M}S_{t-1}$ from the previous year. Equation (T.13) converts P_t to biomass B_t for comparison with the indices I_{it}, where we use the sample weights w_t to represent the population mean weight in year t. The update equation (T.14) for mean age A_t is derived in the Appendix, which also shows that (T.14) is consistent with (T.12). Intuitively, (T.14) states that A_t is computed by adding 1 year to an adjusted value of the previous mean age A_{t-1}. The adjustment depends on the proportion of recruits R_t in the total population P_t. For example, if $R_t = 0$, then $A_t = 1 + A_{t-1}$ because the population includes only survivors that have gained 1 year in age. Similarly, if $P_t = R_t$, then $A_t = 1$ because the population consists entirely of new recruits. Thus, A_t is subject to the constraint

(2.1) $1 \leq A_t \leq A_{t-1} + 1$

The final update equation (T.15) simply defines the survivors remaining after the fishery.

The observation equations (T.16)–(T.17) relate the population states to the measured observations. We assume that the trawl index surveys I_{it} ($i = 1, 2$) are proportional to the population biomass after a fraction f_{it} of the catch has been removed. The parameters q_i calibrate the surveys to biomass units. The lognormal standard error τ_1 is assumed to apply to both surveys with independent standard normal deviates ε_{it}. Similarly, we assign error to the observed age x_t in (T.17) through a lognormal measurement with standard error τ_2 and standard normal deviates η_t.

Our model distinguishes the observed mean age x_t from the population mean A_t. By contrast, we make no distinction

between the observed mean weight w_t and the population mean weight, which we denote by W_t. In effect, we assume that $W_t = w_t$. We could have defined dynamic and observation equations for W_t and w_t, respectively, analogous to (T.14) and (T.17) for A_t and x_t. For example, Schnute and Richards (1998) provide an update equation for population weight moments assuming von Bertalanffy growth. Unlike (T.14), the update equation for W_t requires additional parametric assumptions about the form of the age–weight relationship. We are reluctant to impose such assumptions for Pacific ocean perch. Indeed, we obtained the observations w_{at} from a nonparametric smoother through the raw sample data. Furthermore, given the longevity of Pacific ocean perch and their strongly asymptotic growth, more contrast is possible in mean age A_t than in mean weight W_t.

Equations (T.18)–(T.21) define the likelihood function $L(\mathbf{Q})$ for this stochastic model from the parameter vector $\mathbf{Q}$ in (T.5). Calculation of $L(\mathbf{\Theta})$ involves solving (T.11), (T.16), and (T.17) for the standard normal deviates δ_t, ε_{it}, and η_t. Equations (T.6)–(T.7) allow $\mathbf{\Theta}$ to be expressed in terms of either (σ, τ_1) or (κ, ρ). In the analyses here, we fix ρ (Richards et al. 1997) and allow κ to vary. For estimation, we use the function $\ell(\mathbf{\Theta})$ in (T.22), which is equivalent to twice the negative log likelihood except for a constant K. The quantity $T_1 + T_2$ in (T.22) denotes the total number of surveys in both survey series.

Table 1 omits one technical detail for the Pacific ocean perch case. Two years of age data are missing. We omit these years in the calculations (T.17). Thus, we reduce the likelihood (T.20) by two terms and make corresponding changes in (T.22).

Our complex catch-age analysis of Pacific ocean perch is completely described in Richards et al. (1997), based on the model of Schnute and Richards (1995). The state dynamic

954

Can. J. Fish. Aquat. Sci. Vol. 55, 1998

Fig. 5. Estimates of age 9 recruitment from the simple and complex models, with corresponding 95% confidence intervals (vertical lines). To simplify the display, confidence intervals are indicated for every fifth year only.
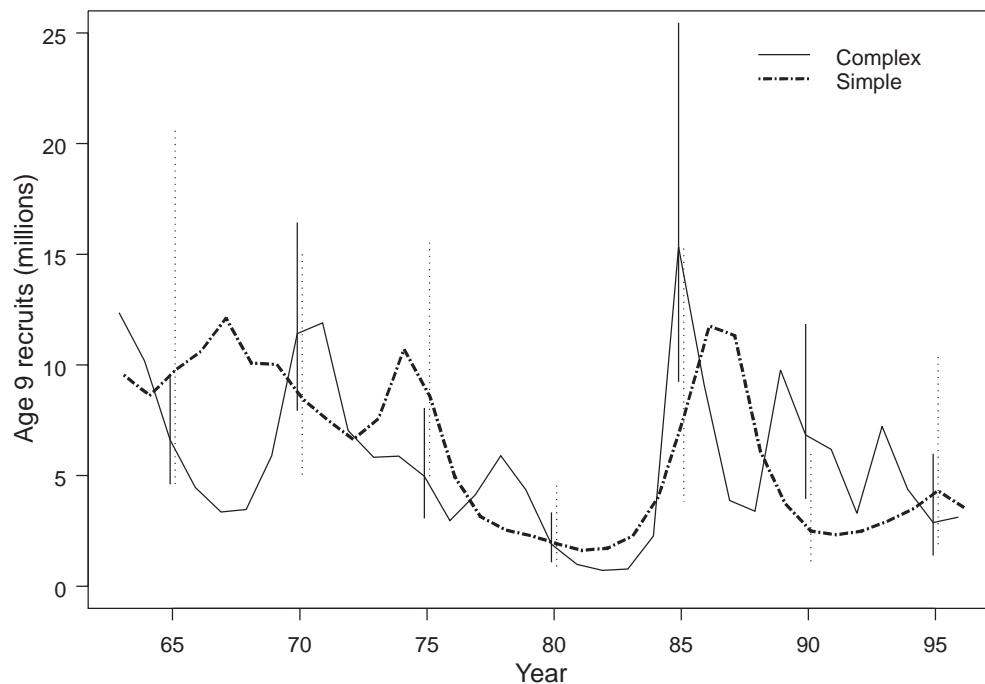
equations are expressed in terms of numbers N_{at} at both age a and time t. Recruitment is not knife-edged; rather, selectivity by the fishery increases asymptotically with age in a given year. Furthermore, the initial states must allow calculation of N_{a1} for each a; the model accomplishes this through estimation of historic recruitments R_{2-a}. The observation equation (T.17) is replaced by a comparison between the predicted proportions at age determined from the state dynamics and the observations portrayed in Fig. 2. We use a multivariate logistic function for this comparison.

For Pacific ocean perch with 34 years of data, the parameter vector Θ in (T.5) for the simple model contains 44 terms, while the comparable parameter vector for the complex model contains 54 terms. For both models, we fix the parameter $\rho = 0.9$, following the rationale in Richards et al. (1997). All other terms in Θ are treated as parameters to be estimated. In particular, we estimate the natural mortality rate M. Computationally, we require procedures to estimate Θ by minimizing $\ell(\Theta)$ in (T.22) and the comparable negative log likelihood for the complex model. We obtain these estimates with the software package AD Model Builder (Otter Research Ltd. 1994), which provides automatic derivatives (Griewank and Corliss 1991) for C++ code and a gradient-based search algorithm. The software also facilitates the computation of confidence intervals for parameter estimates and derived quantities based on normal approximations (Richards et al. 1997, appendix B).

3. Results

Results in Fig. 4 for the complex model indicate that Pacific ocean perch biomass declined during the late 1960s and early 1970s from historical highs in the 1960s. Biomass was relatively stable during the late 1970s and early 1980s and then increased through the early 1990s with a slight decline in 1996.

However, uncertainty increases for the more recent estimates; 95% confidence intervals are broader for estimates for the late 1980s and 1990s. The biomass reconstruction for the simple model is similar. Initial biomass estimates are slightly lower, but the two models produce essentially identical estimates and confidence intervals for the period between the late 1960s and early 1980s. Biomass estimates in the final year are slightly lower for the simple model and the confidence interval is narrower. The two models closely agree on the lower confidence interval for the 1996 biomass, but the simple model appears more certain that the biomass has not increased to high levels.

One reason that biomass estimates are similar for the two models is that estimates of M are also similar. Estimates and standard errors are 0.073 ± 0.016 and 0.070 ± 0.016 for the simple and complex models, respectively. In these types of models, M acts as a scale factor; a higher value of M implies that a higher biomass is required to sustain a given catch.

A feature that distinguishes the trajectories of the two models in Fig. 4 is the smoothness of the trend. For example, the simple model suggests that biomass increased sharply in the period 1985–1987 and then remained relatively stable. By contrast, the selectivity function for the complex model allows recruits of a given year-class to enter the exploitable population over a multiyear period. Essentially, the selectivity function acts to smooth changes in abundance due to recruitment.

Estimated trends in age 9 recruitment are somewhat different for the two models, although the average recruitment is similar (Fig. 5). For the complex model, peak age 9 recruitments are associated with years 1970–1971, 1985, 1989, and 1993. These correspond to relatively large proportions of age 9 fish in the input data (Fig. 2). Recruitment trends are to some extent related to ageing error. For example, the complex model cannot distinguish a strong year-class with ages known to ± 1 year from two or three consecutive above-average year-classes. For

Fig. 6. Estimates of mean age from the simple and complex models and the observed mean age (circles).
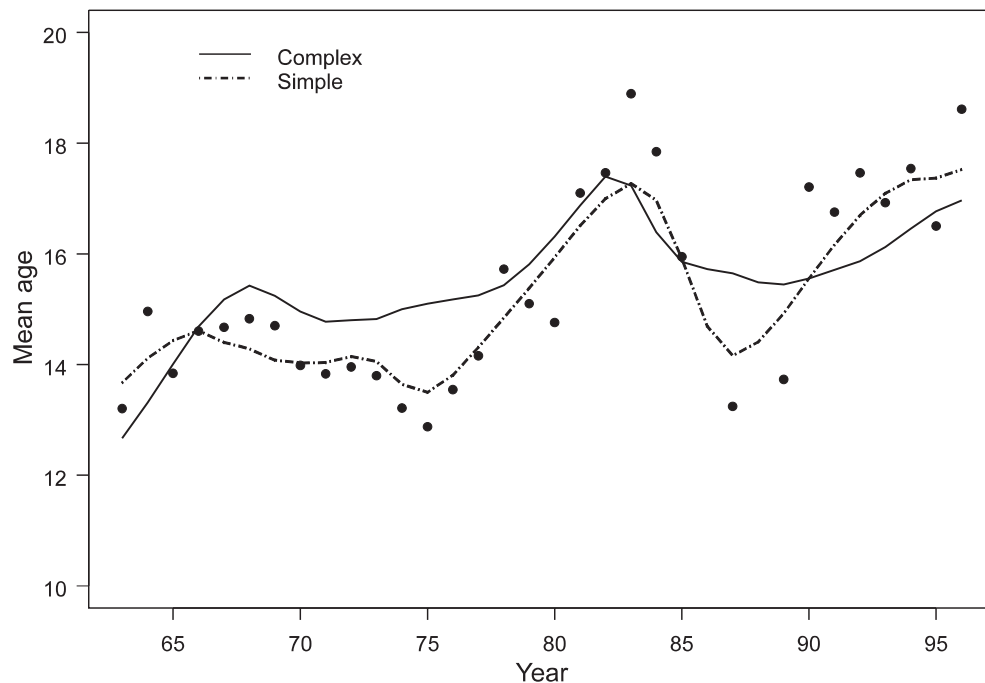
the simple model, peak recruitments lag those of the complex model. However, recruitment estimates are more uncertain for the simple model, as indicated by the broader 95% confidence intervals.

Richards et al. (1997) present a residual analysis for the complex model. For the simple model, the key residuals are those associated with the prediction of mean age. The predicted mean age appears as a smooth function of the observed mean age (Fig. 6). Given the upper limit in the constraint (2.1), the predicted mean age cannot match the large observed changes in mean age in the 1980s; the simple model associates these discrepancies with observation error. Predicted mean ages for the complex model fit the observed data poorly. The complex model overestimates mean age for most years with otolith surface age determination and underestimates mean age for most years with break and burn age determination. This pattern is an artifact of different choices of accumulator age-classes for surface and break and burn data (age 16 and 29 years, respectively). Similarly, the increasing trend in predicted mean age at the beginning of the series for the complex model can be attributed to the model's internal accounting for the transition between the two accumulator age-classes.

4. Discussion

We have distinguished simple from complex models based on the input data and the number of states required to account for the underlying dynamics. For example, a typical catch-age model involves observed age proportions p_{at} for A age-classes and T years, giving a total of $(A - 1)T$ independent data values. In the simple model here, this large data matrix reduces to the vector of T observed mean ages x_t. Similarly, a catch-age model typically involves AT states N_{at} that represent the population at age a in year t. This dimensionality is reduced to $2T$ in our simple model by considering recruits R_t and survivors S_t

only. Simplified model equations accompany these reductions in dimensionality. For example, fishery selectivity is not considered in our simple model.

Model simplicity can also pertain to the number of explicit parameters. For example, our simple model includes the T recruitments R_t in the parameter vector Θ. This number could be reduced considerably by assuming constant recruitment; thus, (T.11) could be replaced by

(4.1) $R_t = R$.

Such a simplified model for the Pacific ocean perch data leads to unrealistically high biomass estimates. For example, under the assumption (4.1), the biomass estimate at the beginning of 1996 is 113 200 tonnes, substantially higher than the upper 95% confidence interval for the corresponding simple or complex model estimates (Fig. 4). Without variable recruitment to explain historical high catches, the model produces consistently high biomass estimates to accommodate the entire catch history. Thus, although assumption (4.1) reduces the number of parameters, it is too simplistic for the data analyzed here.

Our analysis has shown that a model based on mean annual age can reconstruct biomass trends similar to reconstructions from a full age-structured model. While the analyst might rightly prefer a realistic complex model for fisheries stock assessment, a simple model can still provide a useful tool. In particular, it can illustrate the role of specific assumptions in a complex model. For example, the addition of a selectivity function to our complex model does not appear to alter the model biomass estimates. However, the selectivity function and full age structure do contribute to more realistic estimation of annual recruitments.

Ageing error is apparent in the Pacific ocean perch data set (Fig. 2), where it acts to smooth the age proportions. Thus, the abundance of a peak year-class is typically underestimated and adjacent year-class abundances are overestimated (Richards et

956

Can. J. Fish. Aquat. Sci. Vol. 55, 1998

al. 1992). Our complex model does not contain specific adjustments for ageing error. Consequently, it tends to spread the influence of a strong year-class over adjacent year-classes (Fig. 5). To some extent, ageing errors and other sampling errors in the age structure cancel in the mean age calculation (T.1). Thus, our simple model suggests options for investigating stocks where only summary age data are reliable.

Age data, even in summary form, are not available for many fish stocks, whereas weight data are almost always available. Thus, following Schnute and Richards (1998), our update equation for mean age could potentially be replaced or supplemented by analogous equations for mean weight or length. Such update equations could also be extended to acknowledge environmental influences on the growth process. Similarly, observation equations for mean weight or length could be tailored to accommodate sample characteristics. Fish age, when available, generally provides more information about underlying population dynamics than fish size. For example, age of an individual fish increases linearly each year, but its weight typically becomes asymptotic at older ages. For Pacific ocean perch, mean age is a much more informative population characteristic than mean weight.

Preprocessing of the input data is required for any analysis. For the simple model, these requirements are more stringent than for the complex model. For example, the choice of age at recruitment for the simple model may not be obvious. The fishery catch of any fish younger than the age at first recruitment must also be acknowledged. We considered various preprocessing methods for the Pacific ocean perch data and obtained essentially similar biomass estimates. We opted to attribute ageing error to the catch of fish younger than the age at recruitment. In other situations, the prerecruit catch could be removed from the fishery catch, with the age proportions adjusted to sum to 1 over the recruited ages.

It could be argued that our complex model is too simple, with only 10 parameters more than the simple model. Certainly, we could extend our complex analysis to include ageing error, a selectivity function with more than two parameters, or even survival process error as suggested by Schnute and Richards (1995). Of course, there is a trade-off between increased realism and ease of interpretation. In this paper, we have suggested ways of collapsing a complex analysis such that the consequences of added features can be readily understood. We envision a progressive development of complex models, in which the relevance of added complexity is investigated at each stage.

Acknowledgements

References

Archibald, C.P., Fournier, D., and Leaman, B.M. 1983. Reconstruction of stock history and development of rehabilitation strategies for Pacific ocean perch in Queen Charlotte Sound, Canada. N. Am. J. Fish. Manage. **3**: 283–294.

Chilton, D.E., and Beamish, R.J. 1982. Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. Can. Spec. Publ. Fish. Aquat. Sci. No. 60.

Cochran, W.G. 1977. Sampling techniques. 3rd ed. John Wiley & Sons, New York.

Deriso, R.B. 1980. Harvesting strategies and parameter estimation for an age-structured model. Can. J. Fish. Aquat. Sci. **37**: 268–282.

Deriso, R.B., Quinn, T.J., II, and Neal, P.R. 1985. Catch–age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. **42**: 815–824.

Fournier, D., and Archibald, C.P. 1982. A general theory for analyzing catch at age data. Can. J. Fish. Aquat. Sci. **39**: 1195–1207.

Fournier, D.A., and Doonan, I.J. 1987. A length-based stock assessment method utilizing a generalized delay-difference model. Can. J. Fish. Aquat. Sci. **44**: 422–437.

Griewank, A., and Corliss, G.F. (*Editors*). 1991. Automatic differentiation of algorithms: theory, implementation, and application. Society for Industrial and Applied Mathematics, Philadelphia, Pa.

Gudmundsson, G. 1994. Time series analysis of catch-at-age observations. Appl. Stat. **43**: 117–126.

Gulland, J.A. 1965. Estimation of mortality rates. Annex to Arctic Fisheries Working Group Report. ICES C.M. 1965. Doc. No. 3.

Hand, C.M., Workman, G.D., Richards, L.J., Kieser, R., and Perry, R.I. 1995. Bottom trawl and exploratory hydroacoustic survey for rockfish in Queen Charlotte Sound, June 20 to July 7, 1994. Can. MS Rep. Fish. Aquat. Sci. No. 2300.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.

Kendall, M., and Stuart, A. 1979. The advanced theory of statistics. Vol. 2. 4th ed. Macmillan Publishing Co., New York.

Ketchen, K.S. 1981. Reconstruction of Pacific ocean perch (*Sebastes alutus*) stock history in Queen Charlotte Sound. Part II. Catch per unit of effort as a measure of abundance, 1959–79. Can. MS Rep. Fish. Aquat. Sci. No. 1599.

Kimura, D.K. 1981. Standardized measures of relative abundance based on modelling log(c.p.u.e.), and their application to Pacific ocean perch (*Sebastes alutus*). J. Cons. Int. Explor. Mer, **39**: 211–218.

McAllister, M.K., and Ianelli, J.N. 1997. Bayesian stock assessment using catch–age data and the sampling – importance resampling algorithm. Can. J. Fish. Aquat. Sci. **54**: 284–300.

McAllister, M.K., Pikitch, E.K., Punt, A.E., and Hilborn, R. 1994. A Bayesian approach to stock assessment and harvest decisions using the sampling – importance resampling algorithm. Can. J. Fish. Aquat. Sci. **51**: 2673–2687.

Megrey, A. 1989. Review and comparison of age-structured stock assessment models from theoretical and applied points of view. Am. Fish. Soc. Symp. **6**: 8–48.

Methot, R.D. 1989. Synthetic estimates of historical abundance and mortality for northern anchovy. Am. Fish. Soc. Symp. **6**: 66–82.

Methot, R.D. 1990. Synthesis model: an adaptable framework for analysis of diverse stock assessment data. Int. North Pac. Fish. Comm. Bull. **50**: 259–277.

Otter Research Ltd. 1994. An introduction to AD Model Builder for use in nonlinear modeling and statistics. Otter Research Ltd., Nanaimo, B.C.

Pella, J.J. 1993. Utility of structural time series models and the Kalman filter for predicting consequences of fishery actions. *In* Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. *Edited by* G. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn II. Alaska Sea Grant College Program Rep. No. 93-02, University of Alaska, Fairbanks, Alaska. pp. 571–593.

Pope, J.G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. Int. Comm. Northwest Atl. Fish. Res. Bull. **9**: 65–74.

Punt, A.E., and Hilborn, R. 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. Rev. Fish Biol. Fish. **7**: 35–63.

Richards, L.J., and Olsen, N. 1996. Slope rockfish stock assessment for the west coast of Canada in 1996 and recommended yields for 1997. Can. Tech. Rep. Fish. Aquat. Sci. No. 2134.

Richards, L.J., Schnute, J.T., Kronlund, A.R., and Beamish, R.J. 1992. Statistical models for the analysis of ageing error. Can. J. Fish. Aquat. Sci. **49**: 1801–1815.

Richards, L.J., Schnute, J.T., and Olsen, N. 1997. Visualizing catch–age analysis: a case study. Can. J. Fish. Aquat. Sci. **54**: 1646–1658.

Schnute, J. 1985. A general theory for the analysis of catch and effort data. Can. J. Fish. Aquat. Sci. **42**: 414–429.

Schnute, J. 1987. A general fishery model for a size-structured population. Can. J. Fish. Aquat. Sci. **44**: 924–940.

Schnute, J.T. 1994. A general framework for developing sequential fisheries models. Can. J. Fish. Aquat. Sci. **51**: 1676–1688.

Schnute, J.T., and Richards, L.J. 1995. The influence of error on population estimates from catch–age models. Can. J. Fish. Aquat. Sci. **52**: 2063–2077.

Schnute, J.T., and Richards, L.J. 1998. Analytical models for fishery reference points. Can. J. Fish. Aquat. Sci. **55**: 515–528

Stanley, R.D. 1987. A comparison of age estimates derived from the surface and cross-section methods of otolith reading for Pacific ocean perch (*Sebastes alutus*). *In* Proceedings of the International Rockfish Symposium. Alaska Sea Grant Rep. No. 87-2. pp. 187–196.

Sullivan, P.J. 1992. A Kalman filter approach to catch-at-length analysis. Biometrics, **48**: 237–257.

Yamanaka, K.L., Richards, L.J., and Workman, G.D. 1996. Bottom trawl survey for rockfish in Queen Charlotte Sound, September 11 to 22, 1995. Can. MS Rep. Fish. Aquat. Sci. No. 2362.

Appendix. Dynamic equations

In an age-structured population, let N_{at} denote the number of fish in age-class a at the start of year t. Recruits R_t, total population P_t, mean age A_t, and survivors S_t are then given, respectively, by

(A.1) $R_t = N_{1t}$,

(A.2) $P_t = \sum_{a=1}^{\infty} N_{at}$,

(A.3) $A_t = \dfrac{1}{P_t} \sum_{a=1}^{\infty} a N_{at}$,

(A.4) $S_t = P_t - C_t$,

where age-class $a = 1$ corresponds to the recruitment age and C_t is the annual catch. If fishing is not selective on age-classes, it follows that for $a \geq 1$:

(A.5) $N_{a+t,t+1} = e^{-M} \dfrac{S_t}{P_t} N_{at}$.

From (A.1)–(A.2) and (A.5), it follows that

$$P_t = N_{1t} + \sum_{a=1}^{\infty} N_{a+1,t}$$

$$= R_t + e^{-M} \frac{S_{t-1}}{P_{t-1}} \sum_{a=1}^{\infty} N_{a,t-1}$$

$$= R_t + e^{-M} S_{t-1}.$$

This proves (T.12). Similarly, starting from (A.3) and (A.5), the calculation

$$A_t = \frac{1}{P_t} \left[R_t + \sum_{a=1}^{\infty} (a+1) N_{a+1,t} \right]$$

$$= \frac{1}{P_t} \left[R_t + e^{-M} \frac{S_{t-1}}{P_{t-1}} \sum_{a=1}^{\infty} (a+1) N_{a,t-1} \right]$$

$$= \frac{1}{P_t} \left[R_t + e^{-M} \frac{S_{t-1}}{P_{t-1}} (P_{t-1} A_{t-1} + P_{t-1}) \right]$$

(A.6) $\quad = \dfrac{1}{P_t} [R_t + (P_t - R_t)(A_{t-1} + 1)]$

$$= 1 + \frac{P_t - R_t}{P_t} A_{t-1}$$

proves (T.14), where step (A.6) uses (T.12).