Catch-Age Analysis with Auxiliary Information

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

We examined the use of catch-at-age data for estimating population abundance, productivity, and year-class abundance. A review section is included where various published models and our new models are shown to form a cohesive theory of catch-at-age analysis linked by level of model complexity. We developed three new models with different error structures: a log-normal measurement error model, a multinomial measurement error model, and a log-normal process error model. By application to data on Pacific halibut (*Hippoglossus stenolepis*), we show that moderate amounts of auxiliary information, such as fishing effort data or the assumption of a spawner–recruit relationship, are needed to stabilize estimates. The models performed very similarly with moderate amounts of auxiliary information, suggesting a degree of robustness to the underlying error structure. We also developed an extension to classic catch-curve analysis that estimates relative year-class strength reasonably well.

Les auteurs ont étudié l'utilisation de données sur les prises selon l'âge pour évaluer l'importance numérique des populations et des classes d'âge ainsi que la productivité. Ils montrent que les modèles publiés et les leurs forment une théorie cohésive pour l'analyse des prises selon l'âge, théorie liée par le niveau de complexité du modèle. Trois nouveaux modèles sont élaborés, chacun selon une différente structure d'erreurs: un modèle d'erreur de variables log-normales, un modèle d'erreur de variables multinomiales et un modèle d'erreur de processus log-normal. L'application à des données sur le flétan du Pacifique (*Hippoglossus stenolepis*) révèle qu'un nombre modéré d'informations supplémentaires, comme des données sur l'effort de pêche ou une relation hypothétique entre les reproducteurs et les recrues, est nécessaire pour stabiliser les estimations. Les modèles ont réagi de façon semblable à un nombre modéré d'informations supplémentaires, ce qui porte à croire à un certain degré de résistance à la structure d'erreurs sous-jacente. Les auteurs ont aussi perfectionné l'analyse classique de la courbe des prises afin de produire une assez bonne estimation de l'importance numérique relative d'une classe d'âge.

Received August 10, 1984 Accepted January 14, 1985 (J7908) Reçu le 10 août 1984 Accepté le 14 janvier 1985

irtual population analysis (VPA) and its variants (Ricker 1975) provide a powerful tool in fisheries research for estimation of historical population (stock) abundance. The wide usage of VPA can be attributed partly to its limited data requirements: time series data on age-specific catches (in numbers of fish), natural mortality rate, and terminal fishing mortality rates (Gulland 1965). In addition, VPA estimates do not depend on knowledge of effective fishing effort, catchability, gear selectivity, or to a large extent, seasonal patterns in fishing intensity. It does depend, however, on a large cumulative mortality being present between the age of estimated cohort abundance and that cohort's terminal (assumed) abundance (Pope 1972). Traditional VPA is therefore not capable of providing reliable estimates of current year stock abundance.

A number of methods for catch-at-age analysis have been published which produce estimates of current stock size (e.g. Collie and Sissenwine 1983; Doubleday 1976; Dupont 1983; Fournier and Archibald 1982; Lassen 1983; Paloheimo 1980; Pope and Shepherd 1982). In addition, a number of methods have been proposed to update VPA directly through various recursive schemes (some of these are summarized in O'Boyle 1981). In the 1970's, it was established, largely by Doubleday (1976) and Pope (1977), that catch-at-age data alone are

insufficient to estimate stock abundance reliably, because estimated fishing mortality and estimated stock abundance have a large negative correlation. Publications during this decade on catch analysis stress the use of information auxiliary to catch-at-age data for estimation of abundance. Our experience (Deriso and Quinn 1983; Quinn et al. 1984) confirms the need for auxiliary information also in estimating annual surplus production (ASP). Such information takes one of two distinct forms: either as additional data that provide extra information about one or more model parameters, or as additional assumptions about the dynamics of a population. Although an assumption cannot strictly be defined as "information," we use the term in the sense that an assumption provides extra structure in the model.

In this paper, we quantify the amount of auxiliary information needed to stabilize estimates of Pacific halibut (*Hippoglossus stenolepis*) abundance and productivity. We use fishing effort data to provide information about fishing mortality rates, and we assume a relationship between spawners and recruits to provide information about year-class strength. We also discuss the role that assumptions about sources of random error play in structuring our analysis, and we quantify the effects of such assumptions on our estimates. The proliferation of catch-at-age methods published in recent years motivated us to also provide a

review section where we examined the relationship between various methods. We developed new methods in our attempt to make catch-at-age analysis theory more cohesive. Our aim is to provide an explanation of catch-at-age analysis which concentrates on our proposed models and describes the major aspects of some important existing models.

Model Review and Development

Catch-at-age models can be ranked in a hierarchy of increasing complexity. Beginning with simple models that require several restricting assumptions, we proceed to more complex models that demand fewer assmptions but have more parameters to be estimated. We define models in terms of predicted catch in numbers of fish of reference age a in year t, denoted C(t, a). The actual observed catch is denoted C'(t, a).

Catch Curve Analysis

Catch curve regression is based on perhaps the most elementary catch-at-age model (see Ricker 1975, Chap. 2, for a full discussion of such curves). Here, both recruitment and total mortality rate are assumed to be constant during the fishable life of all cohorts present in a random sample of catch, taken during some particular year. Exploitation fraction is assumed to be the same for all cohorts above some recruitment age. Thus, predicted catch is given as

(1)
$$C(t, a) = \mu N(t, a)$$

where μ = exploitation fraction and N(t, a) = abundance of fish in the population with reference age a in year t. Also, abundance of each year-class can be related back to recruitment as

(2)
$$N(t, a) = \exp(-Za)N(t - a, 0)$$

where Z = total annual mortality rate and age 0 is taken here to be the reference age of recruitment into the fishery. Substitution of expression (2) into (1) and taking natural logarithms leads to the familiar catch curve model:

(3)
$$\log (C(t, a)) = \log (\mu N(t - a, 0)) - Za$$

where log-observed catch data from a single year are regressed linearly against age. Note that the normal random error assumption of linear regression analysis allows us to extend the validity of regression of (3) to stocks where recruitment is modelled as a log-normal random variable. In many cases, a standardized field sample is taken (to insure constancy of exploitation sampling, irrespective of age) which is aged and then regressed with (3) to obtain an estimate of Z. Of course, sample data categorized as percentages by age will also suffice.

Relative Abundance Analysis

We developed a catch model that removes two assumptions made in catch curve analysis, but that requires a time series of catch-by-age samples to implement. Recruitment can vary arbitrarily between year-classes, and gear selectivity can vary between ages. We still assume that total mortality rate is constant. Our aim here is to provide a method, independent of effort data, that can be applied to research survey data to estimate relative year-class strength. Fishing effort in the research survey can vary arbitrarily from year to year as long as the survey is a minor source of mortality. We can write

predicted survey catch with this model as

$$C(t, a) = \mu(t, a)N(t, a).$$

Exploitation fraction, $\mu(t, a)$, is assumed to be a product of gear selectivity s(a) and full recruitment survey exploitation $\mu(t)$. A gear selectivity parameter can be estimated for each age, but to simplify matters we have chosen a flexibile gamma-type function to describe the selectivity pattern by age. We write this as

$$s(a) = a^{\alpha} e^{-\beta a} / [\max_{j} (j^{\alpha} e^{-\beta j})]$$

where α and β are gear selectivity coefficients and subscript j ranges over all the surveyed age-classes. The gamma function is a convenient curve form that can assume a variety of patterns commonly found for selectivity: a pattern of increasing selection with age ($\alpha > 0$, $\beta = 0$), a dome-shaped pattern with an intermediate age of maximum selection ($\alpha \neq 0$, $\beta \neq 0$), and equal selectivity for all ages used in the analysis ($\alpha = 0$, $\beta = 0$). Note that the curve is scaled so that s(a) equals unity for the age(s) of full selectivity. This is necessary to make the exploitation fraction well-defined.

Survey catch predicted by our model is a natural extension of catch curve analysis. Analogously to equation (3), predicted catch is given as

(4)
$$\log(C(t, a)) = \log(\mu(t)s(a)N(t-a+1, 1)) - Z(a-1)$$

where reference age 1 is chosen as recruitment age (since the gamma function passes through the origin). We cannot estimate absolute abundance of recruits in equation (4) because abundance and exploitation appear in this equation only as a product of terms; for example, an arbitrary scaling factor can be multiplied to abundance and then exploitation divided by that factor and equation (4) would remain valid. Only by relating total mortality (Z) to exploitation (μ) can we expect to obtain estimates of absolute abundance, as we shall see in methods given later.

We can estimate relative abundance of year-class strength with the model above. It is convenient to structure this estimation problem in terms of the predicted proportion, p(t, a), of fish aged a yr old caught in the survey in year t as a proportion of total catch that year. This structure allows us to eliminate exploitation parameters from consideration, since predicted proportion can be written as

(5)
$$p(t, a) = \frac{a^{\alpha} \exp(-\beta * a) N(t - a + 1, 1)}{\sum_{j=1}^{a_{\text{max}}} j^{\alpha} \exp(-\beta * j) N(t - j + 1, 1)}$$

where a_{max} is the maximum reference age of fish to be analyzed from survey catches and $\beta^* = \beta + Z$. Note that the number of fish randomly chosen to be aged from the sample catch can vary arbitrarily from one year to the next and it does not need to be related in any fashion to the total number of survey-caught fish. For example, it may be convenient to age a fixed number of fish each year. This feature of model flexibility is available because estimates of relative year-class strength (and α , β^*) are based on the shape of the distribution of catch by age (much like the mortality estimates of catch curve analysis are based on the slope of the distribution of catch by age).

Relative abundance of recruitment can be estimated in several ways from equation (5). We chose in this paper to assume that departures of observed data from predictions of (5) were due to random errors in the aging of fish (cf. Fournier and Archibald

1982), so that estimation is performed by maximizing a multinomial log-likelihood function

(6)
$$\max \sum_{t,a} C'(t, a) \log (p(t, a))$$

where C'(t, a) is the observed catch.

Unknown parameters in the estimation are α , β^* , and all recruitments, N(t,1), present in the data set (with the exception of the last recruit year-class, which is arbitrarily scaled to the relative level (1.0). Observe that total mortality, Z, is not estimable separately from the gear selectivity coefficient, β , in this analysis. If independent information on selectivity of the gear is available in terms of estimates $(\hat{\alpha}, \hat{\beta})$, then we set $\alpha = \hat{\alpha}$ in the model and estimate total mortality simply as $Z = \beta^* - \hat{\beta}$. Alternatively, estimates of mortality can be made by using only ages of fully recruited fish in the analysis; here we set $\alpha = 0$ and $\beta = 0$ in the model and then estimate mortality as $Z = \beta^*$. An application of our method is given later in this paper.

Absolute Abundance Analysis

The next level of complexity in catch-at-age models is to develop structural relationships for fishing mortality rates by age and year. This will allow us the capability of estimating absolute abundance of year-classes and it removes the constant mortality assumption from models given above. Most methods assume the Baranov (1918) catch equations hold, so that

$$C(t, a) = \mu(t, a)N(t, a)$$

$$\mu(t, a) = \frac{F(t, a)}{Z(t, a)}[1 - \exp(-Z(t, a))]$$

$$N(t + 1, a + 1) = N(t, a) \exp(-Z(t, a))$$

$$Z(t, a) = F(t, a) + M(t, a)$$

where N(t, a) = population abundance at the beginning of year t for fish aged a reference years old, F(t, a) = fishing mortality rate in year t for a-yr-olds, and M(t, a) = natural mortality rate of a-yr-olds in year t.

Catch at age is then related to its earlier recruitment abundance by

(7)
$$C(t, a) = \mu(t, a) \exp \left[-\sum_{j=1}^{a-1} Z(t-j, a-j) \right] \times N(t-a+1, 1).$$

Equation (7) forms the relationship employed in most models. There are too many parameters to be estimated in equation (7) from catch information alone. We assume that fishing mortality is separable into a product of an age-specific selectivity coefficient, s(a), and a full-recruitment fishing mortality, f(t), following Doubleday (1976), Fournier and Archibald (1982), Pope (1977), and Pope and Shepherd (1982):

$$F(t, a) = s(a)f(t)$$

where s(a) = 1 for at least one age (to insure fishing mortality rates are well-defined). The separability assumption is of fundamental importance in those models, since it reduces the number of unknown fishing mortality parameters from $A \times T$ unknowns (A = number of ages, T = number of years of data) to less than A + T unknowns (T fishing mortality rates and fewer than T age-specific selectivity coefficients). Parameter estimation is thus feasible, especially when we assume values known for natural mortality. Selectivity can either be estimated by a smooth curve (as given before in equation (4), or as in Fournier

and Archibald 1982), or age-specific coefficients can be estimated, as in most models.

Observed catch-at-age data are assumed to differ from predictions in (7) by a log-normal random variable (following Doubleday 1976), and thus, nonlinear least squares can be applied to

(8)
$$\min SSQ(\text{catch}) = \sum_{t,a} (\log C'(t, a) - \log C(t, a))^2,$$

the negative part of a log-likelihood equation. The SSQ is called the residual sum of squares. A somewhat simpler, though higher variance, sequential scheme is employed in Pope (1977).

Analysis with Auxiliary Information

In many recent models, auxiliary information is employed as a means of increasing precision of parameter estimates. The assumption that fishing effort is proportional to full-recruitment fishing mortality is one way to introduce auxiliary information into equation (7) (e.g. in Dupont 1983; Paloheimo 1980). That assumption reduces by (T-1) the number of parameters to be estimated (one catchability coefficient, q, instead of all the f(t) parameters). The main weakness of that approach is that effective fishing effort is seldom known precisely. And, in any case, it is likely that catchability varies from year to year in many fisheries (such as the setline halibut fishery). Fournier and Archibald (1982) suggested an alternative by assuming that the relationship between fishing mortality and fishing effort is not exact, but the difference can be modeled by the log-normal distribution

$$\epsilon_1(t) = \log f(t) - \log (qE(t))$$

where $\epsilon_1(t) = \text{normal } (0, \Delta_1^2)$ random variable, q = catchability coefficient, and E(t) = observed fishing effort. This implies that we add to the minimization criterion in (8) an auxiliary sum of squares term:

$$SSQ(effort) = \lambda_1 \sum_{t} [\epsilon_1(t)]^2$$

where λ_1 is the ratio of variances (variance of observed logarithm catch from that predicted in (7) divided by the variance of observed logarithm effort, Δ_1^2). We consider λ_1 to be a weighting term that adjusts the amount of influence of auxiliary information. For example, if we set λ_1 to a sufficiently large number, then the minimization criterion is forced to set fishing mortality proportional to fishing effort; the catch-age procedure converges (as $\lambda_1 \rightarrow \infty$) to the constant catchability procedure in Paloheimo (1980).

We can carry this notion of adding an auxiliary sum of squares term to any type of auxiliary data available (such as for fish density estimates from survey cruises). Our study also considers stock—recruitment as another possible source of information, which adds to the structure of our model. Following Fournier and Archibald (1982), we assume that recruitment is based on a Ricker spawner—recruit function with log-normal random departures:

$$\epsilon_2(t) = \log N(t+k, 1) - a - \log (S(t)) + bS(t)$$

where $\epsilon_2(t)$ = normal $(0, \Delta_2^2)$ random variable, a and b = stock-recruit coefficients, S(t) = spawning stock egg production in year t, and k = number of years for young to reach recruitment age. The spawning stock S(t) is the sum over all ages of (N(t, a)e(a)), where age-specific net fecundity, e(a), is from Quinn (1981) and abundance, N(t, a), is estimated

simultaneously in the catch-at-age model. We add to our minimization criterion in (8) an auxiliary sum of squares term:

$$SSO(spawn) = \lambda_2 \sum [\epsilon_2(t)]^2$$

where λ_2 is the ratio of variances (variance of observed logarithm catch from that predicted in (7) divided by the variance of the stock-recruitment relationship). By setting λ_2 to a sufficiently large number, we force recruitment to be a deterministic function of spawning stock (as in the method developed by Beddington and Cooke 1981).

The SSQ(spawn) expression above is not technically the correct contribution to our minimization criterion if maximum likelihood is our sole objective. The problem here is that neither recruitment nor spawners are observed directly, and thus, we believe the appropriate objective function is a marginal likelihood function where we integrate over the distribution of random variables $(\epsilon_2(t))$, a prohibitive task on the current generation of computers. This problem is perhaps not well appreciated, but it is common whenever additional model structure involves nonobserved quantities. On the other hand, the expression given seems to us a sensible approach to take.

Our catch-at-age model is now developed to a level of complexity where the problem is to find

(9)
$$\min SSQ(catch) + SSQ(effort) + SSQ(spawn)$$

which reflects a model with the following principal assumptions:

- (a) fishing mortality is separable into an age-dependent factor, selectivity, and a year-dependent factor, full-recruitment fishing mortality rate;
- (b) full-recruitment fishing mortality is proportional to fishing effort times a log-normal random variable;
- (c) catch is given by a Baranov catch equation times a log-normal random variable;
- (d) recruitment is given by a Ricker spawner-recruit function times a log-normal random variable;
 - (e) natural mortality is fixed at an assumed value;
 - (f) variance ratios, λ_1 and λ_2 , are fixed at assumed values.

Multinomial Measurement Error Model

Our analysis will focus on equation (9), as well as two other related models. These other models reflect consequences of changing assumption (c), which assumes that our observations of catch are affected by log-normal measurement errors. Our first alternative model is to assume that measurement errors are the consequence of aging errors in a random sample design (cf. Fournier and Archibald 1982). The multinomial distribution is appropriate in this case, so we could replace the SSQ(catch) term in equation (9) by expression (6). Instead, we find it convenient for our computer software to substitute the asymptotically equivalent chi-square criterion instead of expression (6). Our minimization criterion here is

(10)
$$\min \sum_{t,a} \frac{\left[C'(t,a) - C(t,a)\right]^2}{C(t,a)} + SSQ(effort) + SSQ(spawn).$$

Process Error Model

Process error can affect predictions of catch. In our second alternative model we assume that observed catches are measured precisely as being the true catches, but that process error affects our predictions of catch in a specific way. We assume that true exploitation fraction differs from predicted exploitation by a log-normal random variable. Failure of assumption (a) can cause such a process error when true fishing mortality differs from that predicted with the separability assumption by an approximate log-normal random variable. In this model, forward cohort analysis is used to approximate abundance (conditional on parameters for year-class recruitment) and the predicted catch is calculated as

$$\tilde{C}(t, a) = \frac{s(a)f(t)}{s(a)f(t) + M} \times [1 - \exp(-s(a)f(t) - M)]N(t, a)$$

where

$$N(t, a) = N(t - a + 1, 1) e^{-M(a-1)}$$
$$- \sum_{j=1}^{a-1} C(t - j, a - j) \exp(-Mj + M/2).$$

If natural mortality varies by age or year, these equations can be easily generalized. Our minimization criterion for this model is

(11)
$$\min S\tilde{S}Q(\operatorname{catch}) + SSQ(\operatorname{spawn})$$

where

$$S\tilde{S}Q(\text{catch}) = \sum_{t,a} [\log \tilde{C}(t, a) - \log C'(t, a)]^2.$$

Equivalently, backward VPA or cohort analysis can be used to calculate predicted catches. We chose forward cohort analysis because of ease of programming. A log-normal error structure can be dropped for a multinomial distribution to obtain a process error catch model, similar to Dupont (1983), where observed catches differ from predictions because of the stochastic nature of the fishing process itself.

The three complex models evaluated in our study (equations 9, 10, 11) all have the same number of parameters. Give (A) age-classes and (T) years of data, there are (T) full-recruit fishing mortality parameters, (A + T - 1) year-class recruitment parameters, (A - P) selectivity coefficients (one for each age, except the last P ages for fully recruited fish where selectivity is set to unity), one catchability coefficient, and two spawner-recruit function parameters. This is a total of (2T + 2A + 2 - P) parameters to be estimated from (AT + T) pieces of data (catch-at-age and fishing effort data). Natural mortality rate is chosen at an assumed value in this study (M = 0.2), since reliability of estimates for that parameter seem especially poor (T, J, Quinn II, R, B, Deriso, and P, R, Neal, unpubl. data).

Model Performance: Data and Methods

The models (9-11) were exercised with Pacific halibut catch-age data. Sampling techniques and the data are given by Quinn et al. (1983) and a sensitivity study of the data is described in Deriso and Quinn (1983). The various models were combinations of no, low, medium, and high values of λ for the catch-effort and spawner-recruit sum of squares and the three error-structure formulations (equations 9, 10, and 11).

The first set of exercises were performed on 1967–82 data. The models were applied to this current data set to investigate the robustness of the technique to the influence coefficients (λ 's) for the various sums of squares. In addition, the bootstrapping technique (Efron 1982) was applied to investigate the amount of variability in the estimates.

The second set of exercises were performed on historical

catch-age data (years 1935–70). Estimates of model parameters were compared with those from cohort analysis (Hoag and MacNaughton 1978), which is known to be valid for accurate historical data. We have reasons to doubt complete reliability of our historical age composition data, but we believe cohort analysis estimates from that data constitute the most reliable stock estimates currently available to us. The focus of these exercises was to investigate the accuracy of most recent estimates, as defined below, from the models as compared with the cohort analysis benchmark. Twenty-two data sets of 15 yr of catch-age data were constructed starting with 1935 (1935–49) for the first data set, 1936-50 for the second data set, ..., 1956-70 for the twenty-second data set). Catch-age analysis was performed on each data set and estimates were computed for stock abundance, productivity, and other characteristics for each year of the data set, including those for the latest year, the "most recent estimates." By this procedure, we can imagine that the year is 1950, for example, and we are trying to estimate current stock abundance and productivity using one of the models (9, 10, 11); in retrospect, we can determine the error of the most recent estimates in 1950 by comparison with those from cohort analysis.

Four measures of error of the most recent estimate across data sets were considered: two measures of variability (average absolute error and average absolute fractional error), one measure of bias (average fractional error), and one measure of robustness (maximum absolute error). The average absolute fractional errors are shown later and were calculated as

$$\frac{1}{N} \sum_{i} \frac{|X_i - Y_i|}{Y_i}$$

where N estimates of a particular annual quantity are compared between a model (X_i) and cohort analysis (Y_i) . In addition, the average error for the last 4 yr for each data set was calculated to assure that a designated "good" model for the most recent year was also good for the most recent past as well.

Life history features of Pacific halibut are used in the models. Total catch by age of the entire Pacific halibut population was used, because halibut is a migratory species. A generalization of catch-age analysis for migratory populations is in progress to obtain estimates for geographic regions. Natural mortality is assumed to be 0.2 for all years and ages. Only ages 8-20 are included in the analysis, corresponding to our definition of the adult population. Fish less than 8 yr old are not as well represented in the commercial catch and they are subject to poorly quantified mortality from incidental fisheries. Halibut older than age 20 are also not abundant in the catch and they are subject to possibly higher aging errors than younger fish. Based on previous studies (Quinn et al. 1984), fish aged 15-20 are assumed to be fully recruited. In 1973, the minimum commercial size limit was raised; in the model, this is taken into account by having separate selectivity and catchability parameters before and after 1973. The assumed fishing effort – mortality and spawner-recruit relationships are based on previous studies: a Ricker spawner-recruit relationship is supported by analysis in Deriso (1985), while catchability, the ratio of fishing mortality to effort, is seen to be stable over most time intervals in Deriso and Quinn (1983, fig. 3).

After a model is fit to the data, estimates of model parameters are synthesized into the following fundamental population estimators on an annual basis: biomass and surplus production of the total population, biomass and surplus production of the exploitable population, year-class strength (abundance of age 8

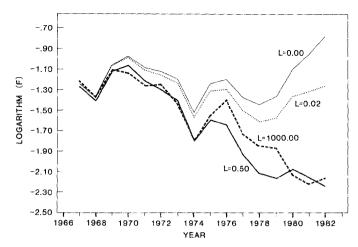


Fig. 1. Logarithm of full-recruitment annual fishing mortality estimated with model (9) for four values of λ_1 (L = 0.00, 0.02, 0.50, 1000.00).

fish), and fishing mortality of fully recruited fish. Some of these terms may not be familiar to the reader. The exploitable population is calculated by summing over all age-classes, the product of age-specific abundance times the proportion of this age-class fully vulnerable to fishing gear (the s(a) coefficient). Annual surplus production represents the annual change in biomass (or exploitable biomass) adjusted for removals by the fishery; it is calculated as the (exploitable) biomass at the start of the next year minus the (exploitable) biomass at the start of the current year plus annual catch.

Model Performance with Current Data

The first part of this set of exercises is to investigate the robustness of catch-age analysis to the choice of λ in the auxiliary sums of squares. Current data from years 1967-82 were used, because during this period, there was good contrast in fishing effort. First, the log-normal error structure in equation (9) was investigated with the fishing effort sum of squares activated, while the spawner-recruit component λ_2 was fixed at zero. Several values of the fishing effort λ_1 between 0 (no relationship between fishing effort and mortality) and 1000 (essentially exact relationship between fishing effort and mortality) were selected and the catch-age model was fit to the data for each λ_1 . Intermediate values of λ_1 between 0.1 and 1.0 produced nearly identical estimates of full-recruitment fishing mortality each year. In Fig. 1, annual estimates of fullrecruitment fishing mortality are plotted for four values of λ_1 : 0, 0.02, 0.5, and 1000. The estimates do not differ much in the long-term between a λ_1 of 0.5 and a λ_1 of 1000, but short-term differences do occur, attributable to annual changes in apparent catchability. Both sets of estimates differ markedly in later years from those using a λ_1 of 0, while they are all similar for the earlier years. The convergence in the earlier years shows that fishing mortality is well-determined by catch data, which is similar to the convergence of fishing mortality estimates found as a property in cohort analysis. This exercise was repeated for the chi-square error structure in equation (10) and for the log-normal process error structure in equation (11) with essentially the same result, except that for equation (10) a larger value of λ_1 was needed to implement the exact relationship.

In these exercises, we found that results of catch-age analysis are robust to the selection of λ_1 as long as intermediate values

Table 1. Bootstrap results of estimates of five model parameters for the years 1967–82. For each parameter-year combination, the original estimate, the bootstrap mean, and the bootstrap standard deviation are given. Estimates of biomass and production are in thousands of tonnes; estimates of year-class strength are in millions of age 8 fish. B = biomass, EB = exploitable biomass, ASP = annual surplus production, EASP = exploitable annual surplus production, YC = year-class strength.

Year	В	EB	ASP	EASP	YC
1967	146.36	97.66	11.49	17.12	2.78
	146.62	97.44	11.47	17.12	2.71
	2.87	3.44	1.03	0.80	0.09
1968	134.68	91.61	22.71	18.74	2.18
	134.92	91.39	23.02	18.91	2.20
	2.90	3.25	1.34	0.75	0.07
1969	138.30	91.27	11.56	17.00	3.51
	138.85	91.22	11.68	17.18	3.57
	3.35	3.26	1.35	1.03	0.14
1970	125.83	84.24	13.96	16.86	2.31
	126.50	84.37	14.23	16.96	2.28
	3.89	3.12	1.39	0.93	0.12
1971	117.11	78.43	14.59	16.58	2.50
	118.05	78.66	14.69	16.75	2.44
	4.90	3.43	1.57	1.08	0.15
1972	112.26	75.57	15.25	6.70	2.19
	113.31	75.97	15.50	6.83	2.14
	6.13	4.00	1.91	2.30	0.17
1973	109.70	64.46	15.16	13.90	1.98
	111.00	64.98	15.62	14.10	2.00
	7.81	4.33	2.24	1.15	0.19
1974	111.45	64.95	17.24	13.57	1.93
	113.20	65.67	17.75	13.82	1.96
	9.87	5.22	2.91	1.37	0.22
1975	118.59	68.43	18.94	14.44	2.20
	120.86	65.67	19.74	14.80	2.27
	12.58	6.43	3.91	1.75	0.29
1976	125.58	70.92	19.90	15.47	2.57
	128.65	72.24	20.57	15.81	2.58
	16.32	7.98	4.30	2.19	0.39
1977	133.72	74.63	23.54	16.35	2.76
	137.46	76.30	24.41	16.80	2.75
	20.34	10.04	5.12	2.52	0.45
1978	147.73	81.45	18.11	16.03	3.31
	152.34	83.55	18.98	16.47	3.39
	25.21	12.45	4.66	2.83	0.56
1979	157.09	88.73	23.35	17.73	2.98
	162.57	91.27	24.48	18.30	3.15
	29.45	15.18	6.21	3.30	0.59
1980	171.17	97.19	27.63	20.17	3.80
	177.78	100.30	29.48	21.00	3.89
	35.28	18.37	8.66	4.27	0.83
1981	188.40	106.96	23.66	21.82	4.72
	196.86	110.90	25.04	22.72	4.34
	43.57	22.50	7.80	5.03	0.98
1982	200.76 210.60 50.74	117.48 122.32 27.41			3.65 3.62 0.95

are used. Our methodology has also been applied to a stock of Atlantic Moroccan sardine (Sardina pilchardus) by Rami (1984), who also investigated the sensitivity of results to the choice of λ_1 . He found sensitivity results similar to ours for fishing mortality estimates in some years, but, in contrast, his estimates appear extremely sensitive to the choice of λ_1 in other years. The difference in results given here as compared with those in Rami (1984) could be due either to higher variability in his observed fishing effort or to his analysis covering a much shorter time period.

To investigate the variability about the estimated parameters, we applied the bootstrap technique (Efron 1982) to this data set for the log-normal error structure and the catch-effort sum of squares. The essence of the bootstrap technique is to randomly sample with replacement the residuals from the nonlinear catch-age analysis and to sequentially add the sampled residuals to the catch-age and effort data. This process creates a new data set with the same statistical properties as the original data set, and catch-age analysis produces a new set of estimated parameters. Twenty-five new sets of parameter estimates were produced, which can be used to study the empirical distribution of the estimates. In particular, the bias and the variance can be estimated.

Results of the bootstrap technique applied to the halibut data and equation (9) are shown in Table 1. For each yearly parameter of interest, the original estimate, the bootstrap mean, and the bootstrap standard deviation are shown. The difference between the bootstrap mean and the original estimate is an estimate of the bias. The bootstrap standard deviation is an estimate of the standard error of the estimate. For all parameters, the estimated bias is small. The relative error of the most recent estimate is about 20% of the mean and decreases substantially the farther back in time one goes. Thus, catch-age analysis appears to produce reasonable estimates of recent parameters in the sense that the estimates have little or no bias and low variability.

Model Performance with Historical Data

The essence of these exercises is to determine which values for λ_1 and λ_2 and which of the models (9, 10, 11) provide a reliable estimate of a specified annual model parameter. As discussed earlier, we assess reliability of an estimate by comparison with cohort analysis of historical data of year-classes that have complete catch data. For example, catch-age analysis was applied to the 1935–49 data set, as if data beyond 1949 were not available. The estimate of surplus production in 1948 was calculated (surplus production in 1949 cannot be computed without an estimate of biomass in 1950) and compared with the estimate from cohort analysis, which provides a benchmark based on the completion of year-classes present in 1949. This process was repeated for the other 21 data sets. Although these data sets overlap, the purpose of the study is to examine the effect of one new year of data.

For each data set, various combinations of high, medium, low, and no influence of catch-effort and spawner-recruit information were examined. Experience from the previous exercises resulted in values of λ as follows:

Influence	Log-normal (model 9)	Chi-square (model 10)	Log-normal (model 11)
High	1000	1×10^{9}	1000
Medium	0.5	0.5	0.5
Low	1×10^{-7}	1×10^{-7}	1×10^{-7}

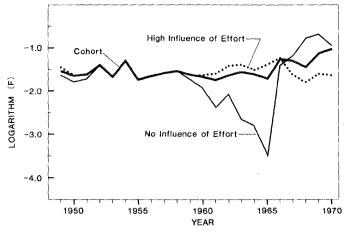


FIG. 2. Logarithm of full-recruitment annual fishing mortality estimates with model (9) for high (and no) influence of fishing effort, along with estimates from cohort analysis. The most recent model (9) estimate from each of the 22 historical data sets is shown.

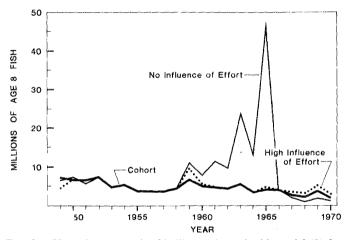


Fig. 3. Year-class strength of halibut estimated with model (9) for high (and no) influence of fishing effort, along with estimates from cohort analysis. The most recent model (9) estimate from each of the 22 historical data sets is shown.

Influence coefficients for a given level of influence (e.g. high) for the catch-effort and spawner-recruit sum of squares were kept the same to simplify interpretation of the results.

To illustrate the year-to-year results, the most recent model (9) estimate of each of the 22 data sets is contrasted with the one from cohort analysis for high and low levels of catch-effort influence and no spawner-recruit influence for the following model parameters: full-recruitment fishing mortality (Fig. 2), year-class strength (Fig. 3), and exploitable surplus production (Fig. 4). Medium influence of catch effort produces similar results to cohort analysis. The figures show substantial deviation of results with no influence of catch-effort information to those from cohort analysis, an indication of estimation instability of catch-age analysis with no auxiliary information. High influence of effort also produces deviation from cohort analysis results, but not nearly as much as no influence. The figures also show relationships between the selected model parameters. Estimated fishing mortality is negatively correlated with yearclass strength and surplus production across data sets with no influence of effort. Because catch is the product of fishing mortality and abundance, roughly the same catch can be obtained by increasing abundance and decreasing fishing

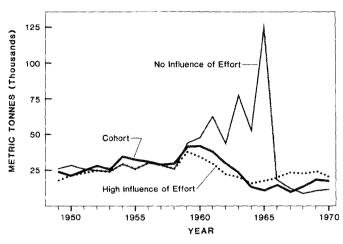


Fig. 4. Exploitable annual surplus production estimated with model (9) for high (and no) influence of fishing effort, along with estimates from cohort analysis. The most recent model (9) estimate from each of the 22 historical data sets is shown.

mortality, or vice versa. Hence, in order to estimate fishing mortality and abundance jointly, some auxiliary information is useful to reduce this inherent correlation. Catch-effort information appears to accomplish this reduction.

Results of the "no influence of effort" analysis in Fig. 2, 3, and 4 show that a wide divergence occurs in the year 1965, and to a lesser extent in the years 1960-64. We believe these disparities are due primarily to departures of age-specific fishing mortality from the assumed separable pattern where age selectivity is assumed constant during the 15-yr time blocks being analyzed. We calculated age selectivity from cohort analysis for each age and year combination in our data set. Estimated selectivity is indeed atypical during the early 1960's; for example, age selectivity of age 11 halibut ranges from 0.86 to 1.13 during the years 1959-65, compared with a range of selectivity from 0.47 to 0.83 for other years. Abnormally high age selectivity of halibut aged 8-12 yr occurs during the early 1960's, followed by a dramatic drop in selectivity during 1966; for example, age selectivity of 8-yr-olds dropped from 0.53 in 1965 to 0.27 in 1966.

The yearly estimates were summarized into two measures of accuracy in order to compare in greater detail levels of influence, model parameters, and error structures. The other measures of error gave essentially the same general results. Results from average absolute fractional error and average fractional error (averaged over twenty-two 15-yr regressions) are given for exploitable annual surplus production (Table 2), exploitable biomass (Table 3), and year-class strength (Table 4). Those tables give the average errors of estimates from each of the three models (9, 10, 11) for all combinations of high. medium, and low λ values in he auxiliary variables, fishing effort, and spawner-recruit relationship. The average absolute fractional error is similar to a coefficient of variation as a measure of precision of parameter estimates, while average fractional error is a scaled measure of bias in parameter estimates, as compared with estimates obtained from cohort analysis.

The need for auxiliary information in our catch-age analysis is clearly indicated by results depicted in Tables 2, 3, and 4. Absolute fractional errors range from 45.6 to 176.8% for the three models when no auxiliary information is included in the analysis. A very low level of influence of auxiliary information

TABLE 2. Percent errors in the estimates of exploitable annual surplus production across twenty-two 15-yr data sets for three models and various combinations of the λ influence coefficients.

λ values		Average	of absolute fract	ional errors	Δvet	age of fractional	errore
Spawn- recruit	Fishing effort	Model (9)	Model (10)	Model (11)	Model (9)	Model (10)	Model (11)
High	High	28.5	26.4	24.3	10.7	10.5	10.0
High	Medium	24.1	29.2	24.5	6.7	3.6	8.7
High	Low	26.8	31.3	24.8	6.2	2.6	7.3
Medium	High	26.1	26.5	21.8	9.7	7.6	8.5
Medium	Medium	18.4	27.4	19.6	8.2	-6.4	0.0
Medium	Low	32.3	40.9	31.7	14.2	-2.9	-16.0
Low	High	26.1	26.1	22.1	9.9	8.0	8.9
Low	Medium	19.5	29.4	19.7	7.8	-9.7	-2.9
Low	Low	153.2	64.6	45.6	126.3	1.6	-44.2
No	No	154.2	64.6	45.6	127.4	1.6	-44.2

Table 3. Percent errors in the estimates of exploitable biomass across twenty-two 15-yr data sets for three models and various combinations of the λ influence coefficients.

λ values		A	. C. J J C	1	A	66		
Spawn- recruit	Fishing effort	Average of absolute fractional errors			Average of fractional errors			
		Model (9)	Model (10)	Model (11)	Model (9)	Model (10)	Model (11)	
High	High	17.3	16.2	15.5	-1.6	7.9	-0.9	
High	Medium	17.1	24.4	15.3	-3.4	1.7	-0.3	
High	Low	19.2	27.0	15.2	-4.2	0.3	-2.2	
Medium	High	17.8	16.7	17.3	-0.2	6.3	-1.5	
Medium	Medium	14.4	14.4	19.1	1.4	-9.1	-10.1	
Medium	Low	19.3	27.5	28.4	5.2	-7.0	-28.3	
Low	High	20.0	19.7	18.9	1.2	8.0	-1.8	
Low	Medium	16.0	23.5	21.1	1.5	-13.0	-12.1	
Low	Low	112.6	54.8	54.2	85.2	-6.9	-54.2	
No	No	113.1	54.8	54.2	85.7	-6.9	-54.2	

TABLE 4. Percent errors in the estimates of year-class strength (abundance of 8-yr-old halibut) across twenty-two 15-yr data sets for three models and various combinations of the λ influence coefficients.

λ values		Average of absolute fractional errors		Average of fractional errors			
Spawn- recruit	Fishing effort	Model (9)	Model (10)	Model (11)	Model (9)	Model (10)	Model (11)
High	High	15.7	20.4	18.1	7.6	14.7	10.1
High	Medium	14.0	20.7	16.6	3.5	3.0	7.6
High	Low	16.6	22.9	16.5	2.4	1.7	5.5
Medium	High	19.9	23.6	20.0	7.5	7.9	7.8
Medium	Medium	20.1	20.5	15.5	7.8	-12.4	-3.0
Medium	Low	21.1	35.1	28.1	11.5	-9.7	-25.0
Low	High	23.6	24.8	23.4	7.5	8.3	7.4
Low	Medium	28.4	30.6	22.1	8.3	-15.5	-6.4
Low	Low	175.7	71.6	57.2	141.6	-1.7	-56.2
No	No	176.8	71.6	57.2	142.7	-1.7	-56.2

does little to improve the error rates. Absolute errors were typically less than 30% when given at least a medium influence of auxiliary information from fishing effort and/or spawner–recruit relationship; the poorest of these cases was usually for a medium spawner–recruit λ and a low effort λ , and the best of these cases was usually when both λ values were set at medium levels. The three models perform at about the same absolute

error rates when at least one medium or high λ is present. With no auxiliary information, model (9) is much less reliable than either of the other two models.

Bias is reduced substantially in models (9) and (11) when auxiliary information is included. Models (10) and (11) gave slight downward biases and model (9) was biased upward for our most precise scenario, where both λ values are set at

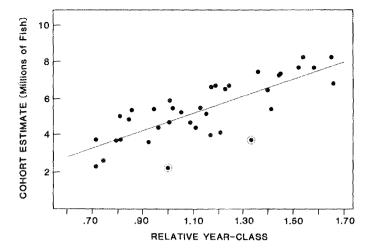


Fig. 5. Estimates of relative year-class strength of age 8 halibut from application of model (6) are compared with year-class estimates from cohort analysis for the years 1935–70; also given is the linear regression line. The most recent year-class estimates (for 1969 and 1970) are indicated by circled points in the figure.

medium levels. Overall, all three models exhibit both positive and negative bias, depending both on the level of λ influence and on the quantity being calculated.

Example Application of Model (6)

Thus far we have relied on rather complex models to estimate year-class strength. In this section, we apply the rather simple extension of catch-curve analysis given in equations (5) and (6) in order to estimate relative year-class strength. This approach can be applied to survey catch data (or to commercial catch data) without our needing to know even the amount of total annual landings.

The model (6) is fitted to Pacific halibut catch-age data obtained from sampling commercial catches of fish aged 8–20 yr from 1935 to 1970. Estimates of relative year-class strength of 8-yr-olds from this application are compared with year-class estimates obtained with cohort analysis in Fig. 5. The linear correlation coefficient between these estimates ($\hat{r}=0.78$) is statistically significant (p<0.01). As seen in Fig. 5, removal of estimates for the most recent year-classes there (1969 and 1970 are circled) would improve the correspondence with cohort analysis; this reflects our expectations, since those recent estimates are based on only one piece of catch-at-age data for 1970 and two pieces for 1969. We are surprised at how well this procedure works here, because fishing mortality changed substantially between 1935 and 1970, while model (6) assumes that mortality is constant.

Discussion

The bulk of this paper is concerned with an evaluation of three complex models (9, 10, 11) and whether auxiliary information is necessary. From our evaluation, it is clear in Tables 2, 3, and 4 that it is necessary to include some auxiliary information in catch-age analysis besides catch-age data. The poor quality of estimates when $\lambda = 0$ confirms a similar conclusion in Doubleday (1976) and Pope (1977).

Our results show that very high λ coefficients where fishing effort borders on a deterministic relationship to fishing mortality and/or recruit is essentially determined by a spawning index

produce estimates about as precise as medium λ values. Initially, this result puzzled us, since estimates (from cohort analysis) of the halibut spawner-recruit relationship (Deriso 1985) and estimates of the fishing effort – mortality relationship (Deriso and Quinn 1983) both exhibit variability. We have two hypotheses for this result: (1) halibut dynamics are sufficiently deterministic that high \(\lambda \) values produce acceptable results and/or (2) high λ values constrain feasible parameter values and thus reduce the sensitivity of the procedure to violations of the (fishing mortality) separability assumption. The second hypothesis is consistent with results in Fig. 2, 3, and 4 that show that the no influence ($\lambda = 0$) results were apparently sensitive to atypical selectivity coefficients during the early 1960's. The first hypothesis is supported by the stable (CV 17%) estimates for survival of the young between 1947 and 1965 (Quinn 1981) and stable catchability coefficient estimates (CV 21%) we get from cohort analysis estimates of fishing mortality. At least some of the imprecision of these estimates is due to measurement errors (Walters and Ludwig 1981). In any case, more biologically realistic assumptions (the medium λ values) did not get us closer to the truth, if we view cohort analysis for the 1949-70 estimates as being true.

The three complex models perform similarly with auxiliary information despite striking differences in the model assumptions about sources of stochasticity in the data. Results in Tables 2, 3, and 4 indicate that it makes little difference if we assume that random errors are due to measurement error in a log-normal form (model 9) or a multinomial form (model 10) or whether they are due to process error in a log-normal form (model 11). We prefer the log-normal forms for catch data (models 9 and 11) because of ease in computer programming and because lognormal forms are also used for auxiliary information. If relative year-class strengths are the estimates sought, then results of model (6) in Fig. 5 suggest that even the complexity of models (9), (10), and (11) may be unnecessary. The trade-off seems basically one of simple models with no auxiliary information for estimating relative quantities or more complex models with moderate influence of auxiliary information for estimating absolute quantities.

Two papers (Collie and Sissenwine 1983; Lassen 1983) consider models with less deterministic structure and more parameters than any of the ones analyzed here. In the first paper, natural random variability is introduced in the survival dynamics of each cohort, whereas in the second paper, fishing mortality is not assumed to be separable into an age factor and a year factor. In both cases, this involves estimating at least $A \times T$ parameters, since each age—year combination has potentially unique interaction. This implies that information auxiliary to catch-at-age data must be used in order to estimate parameters. It also raises the interesting issue as to when a model is over-parameterized relative to the information content of the data base available to analysis. For our study, we have shown the need for auxiliary information in models with much fewer parameters (equations 9–11).

One way to increase the degrees of freedom for catch-age models is by gear stratification. Alton and Deriso (1983) developed and applied a stratified version of the Doubleday (1976) model to Alaska pollock; subsequently, Rami (1984) applied this method to Moroccan sardine. These analyses show that stratification can substantially change abundance estimates, as compared with nonstratified analysis. However, they present no results on whether stratification increases the reliability of parameter estimates.

Computer Software Available

We developed a comprehensive package of computer software CAGEAN (Catch AGE ANalysis) for catch-at-age analysis. CAGEAN includes the three models (9, 10, 11), with options for bootstrapping estimates, stratified gear selectivities, and other bells and whistles. CAGEAN is written in standard ANSI Fortran 77 and should be operable on most minicomputers and mainframes with little modification; currently, the package is working both on a Prime 550 minicomputer and a Cyber 7600 mainframe. (For a free copy of CAGEAN and user manual, please write to one of us.)

Acknowledgments

We thank D. McCaughran for reviewing this paper. Comments by two anonymous reviewers are appreciated.

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