A General Theory for Analyzing Catch at Age Data

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We present a general theory for analyzing catch at age data for a fishery. This theory seems to be the first to address itself properly to the stochastic nature of the errors in the observed catch at age data. The model developed is very flexible and accommodates itself easily to the inclusion of extra information such as fishing effort data or information about errors in the aging procedure. An example is given to illustrate the use of the model.

Key words: cohort analysis, virtual population analysis, maximum likelihood estimation, aging errors

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L'article qui suit contient une description d'une théorie générale applicable à l'analyse de données sur les prises par âge dans une pêcherie. Pour la première fois, semble-t-il, cette théorie tient compte de la nature stochastique des erreurs que contiennent ces données. Très flexible, le modèle se prête facilement à l'inclusion de données supplémentaires telles que l'effort de pêche ou des renseignements sur les erreurs dans la détermination de l'âge. L'emploi du modèle est illustré à l'aide d'un exemple.

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The use of catch at age data for estimating various parameters associated with fish populations dates from the work of Fry (1949), Jones (1964), Gulland (1965), and Pope (1972). These early methods were not stochastic, that is, they did not consider the form of the observational errors which gave rise to the observed catch data or try to extract the additional information which can be gained by analyzing the various cohorts simultaneously. Doubleday (1976) produced a model which dealt with both of these aspects of the problem. Doubleday's approach is somewhat unsatisfactory, however, as a result of the arbitrary nature in which the stochastic element is introduced into the model.

Let C_{ij} be the true catch of age class j fish in year i, and O_{ij} be the estimate of C_{ij} which is to be used in the catch at age model. Doubleday assumes that the variance of the random variable $\log(O_{ij})$ is approximately independent of the value of C_{ij}. In fact, under the most natural assumptions about the stochastic nature of the process which generates the O_{ij}, it would follow that the variance of $\log(O_{ij})$ tends to infinity as the percentage which that age class forms of the catch tends to zero.

Recently Paloheimo (1980) has extended Doubleday's results by including fishing effort information into the estimation procedure. However, the method of introducing the stochastic element into the model remains somewhat unsatisfactory.

The purpose of this paper is to introduce a general model for analyzing a time series of catch at age data for a fishery. When designing such a model, two objectives must be kept in mind. First the model should have the correct stochastic orientation. This means that both the information submitted to the model and the underlying processes which the model describes are subject to error, and that the model should attempt to allocate these errors in a reasonable fashion. Secondly, the model should be flexible; that is, the user should be able to include any information or even opinion which he has into the model and observe its effect on the solution obtained. In the present situation such information could include among other things, fishing effort information, accuracy of aging techniques, accuracy of the estimates of total landings, existence of a stock–recruitment relationship, the effect of environmental factors on recruitment, or changes in size at age of the fish.

The model described here gives methods of combining this information in a systematic way with the catch at age data in order to provide an analysis of the past behavior of an exploited fish population.

The problem of constructing a model for analyzing catch at age data divides itself naturally into three independent parts. First is the assumption of the kind of error structure inherent in the catch at age data and the formulation of the appropriate likelihood function. Second is the adoption of some relationship between the true catches and the instantaneous mortality rates. Finally, there is the assumption of regularities in the instantaneous mortality rates. The analysis of the problem from this point of view leads to a clearer understanding of the role played by each constituent. In addition the resulting model is more flexible in that the structure of any constituent

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can be easily modified if desired without changing the other constituents.

Finally, an important point should be emphasized which is too often overlooked in the design or application of models for analyzing fisheries data. When attempting to apply an existing model to a new set of fisheries data, one almost invariably encounters some new contingency which calls for major or minor revisions of the model. For this reason a model should not be regarded as a final finished product but rather as a flexible framework which can always be modified should the situation require it. We have organized this paper so it follows as closely as possible the actual development of the model. Symbols used are given in the Appendix.

1. The Basic Model

In section 1 the basic model using only catch at age data is developed and the calculations necessary for constructing the computer program are described. This section contains by far the most involved calculations. Once they have been carried out, extra information about the fishery can be incorporated into the model by adding rather simple terms to the log-likelihood function.

In many catch at age analysis models the basic data or set of observations is assumed to be the number of fish caught at each age. It is, in fact, more reasonable to construct a model based on estimates of the total catch (in numbers of fish) and on estimates of the percentage of the catch at each age. This point of view has several advantages for the construction of a stochastic model:

1) There are in fact errors both in estimating total catch and in estimating percentages at age.

2) The errors in estimating the percentages at age have unequal variances and are correlated, and this point of view makes it possible to construct an analytical framework to deal with this situation.

3) It becomes simple to incorporate information about errors in the age estimation procedure into the model.

Let r denote the number of age classes in the fishery and n be the number of years of fishery information. Suppose that in each year i a number of fish are picked out and aged and that S_{ij} are the number of fish observed to be of age j in year i.

Let O_i be the estimated number of fish caught in year i, C_i be the actual number of fish caught in year i, and P_{ij} be the actual percentage of the fish of age j in the catch in year i.

We make the following assumptions:

1) The random variables S_{ij} and O_i are independent.

2) $O_i = C_i \exp(\epsilon_i)$

where the ϵ_i are independent normally distributed random variables with mean 0 and variance σ^2.

3) The S_{ij} are obtained by taking a random sample of the fish and aging it and that there are no errors in the aging procedure.

Given the above stochastic assumptions it follows that the likelihood function for the parameters P_{ij}, C_i, and σ is equal to a constant times

$$1.0 \qquad \prod_{i,j} P_{ij}^{S_{ij}} \prod_i \frac{1}{\sqrt{2\pi}\sigma} \exp\left[-\frac{1}{2}\left(\frac{\log O_i - \log C_i}{\sigma}\right)^2\right].$$

Taking the natural logarithm of 1.0 and ignoring the constant terms, one obtains the log-likelihood function

$$1.1 \qquad \sum_{i,j} S_{ij} \log P_{ij} - \sum_i \frac{1}{2}\left(\frac{\log O_i - \log C_i}{\sigma}\right)^2 - n \log \sigma.$$

Note for later reference that for each i, j the constraints

$$1.2 \qquad \sum_j P_{ij} = 1, \quad P_{ij} > 0$$

hold.

At this point there is no link between the observations S_{ij} and O_i and the underlying process being studied, the exploitation of a fish population. This link is established by the so-called catch equations.

Let F_{ij} and M_{ij} denote the instantaneous fishing mortality and natural mortality for fish from age class j in year i, and N_{ij} denote the number of fish in age class j in year i.

Then we shall assume that the catch equations (Ricker 1975)

$$1.3 \qquad C_{ij} = \frac{F_{ij}}{F_{ij} + M_{ij}} \left[1 - \exp(-F_{ij} - M_{ij})\right] N_{ij}$$

$$1.4 \qquad N_{i+1,\,j+1} = \exp(-F_{ij} - M_{ij}) N_{ij}$$

hold.

If the last year class is totally fished out, then equation 1.3 becomes

$$1.3\text{A} \qquad C_{ir} = \frac{F_{ir}}{F_{ir} + M_{ir}} N_{ir}$$

1.5 For $1 \le i \le n-1$, $1 \le j \le r-1$, define the quantities Φ_{ij} by

$$\begin{aligned} \Phi_{ij} = {} & \log(F_{ij}) - \log(F_{i+1,\,j+1}) \\ & - \log(F_{ij} + M_{ij}) \\ & + \log(F_{i+1,\,j+1} + M_{i+1,\,j+1}) \\ & + \log[\exp(F_{ij} + M_{ij}) - 1] \\ & - \log[1 - \exp(-F_{i+1,\,j+1} - M_{i+1,\,j+1})]. \end{aligned}$$

Equations 1.3 and 1.4 imply that the quantity Φ_{ij} satisfies the equation

$$\begin{aligned} 1.6 \qquad \Phi_{ij} &= \log(C_{ij}/C_{i+1,\,j+1}) \\ &= \log(P_{ij}) + \log(C_i) \\ &\quad - \log(P_{i+1,\,j+1}) - \log(C_{i+1}). \end{aligned}$$

If the last age class is totally fished out, then for $j = r-1$ equation 1.5 becomes

$$\begin{aligned} 1.5\text{A} \qquad \Phi_{i,\,r-1} = {} & \log(F_{i,\,r-1}) - \log(F_{i+1,\,r}) \\ & - \log(F_{i,\,r-1} + M_{i,\,r-1}) \\ & + \log(F_{i+1,\,r} + M_{i+1,\,r}) \\ & + \log[\exp(F_{i,\,r-1} + M_{i,\,r-1}) - 1]. \end{aligned}$$

Thus the log-likelihood function for the parameters P_{ij}, C_i, is given by the expression 1.1 subject to the n constraints 1.2 and the $(n-1)(r-1)$ constraints

$$1.7 \qquad \log P_{ij} + \log C_i - \log P_{i+1,\, j+1} - \log C_{i+1} = \Phi_{ij}$$

where the quantities Φ_{ij} depend on the instantaneous fishing mortalities F_{ij} and M_{ij}.

If we consider the quantities S_{ij} and O_i to be given, then the expression 1.1 depends on the $nr+n$ quantities P_{ij} and C_i. The maximum likelihood solution to the problem is given by those values of P_{ij} and C_i which maximize 1.1 subject to the $n+(n-1)(r-1)$ constraints 1.2 and 1.7.

This is a large problem and it is impractical to solve it as formulated. However, it is possible to eliminate all the constraints as follows.

Let $\beta_{ij} = \log (P_{ij}C_i/O_i)$
and $\gamma_i = \log (O_i)$.
Then $\log (P_{ij}C_i) = \log (P_{ij}C_i/O_i) + \log (O_i) = \beta_{ij} + \gamma_i$.
Thus the system of constraints 1.7 can be rewritten as

$$1.8 \qquad \beta_{ij} + \gamma_i - \beta_{i+1,\, j+1} - \gamma_{i+1} = \Phi_{ij}.$$

Also it is easily verified that

$$[\log (O_i) - \log (C_i)]^2 = \left\{\log \left[\sum_j \exp(\beta_{ij})\right]\right\}^2$$

and

$$P_{ij} = \exp(\beta_{ij}) \Big/ \left[\sum_j \exp(\beta_{ij})\right]$$

so that 1.1 can be rewritten as

$$1.9 \qquad \sum_{i,j} S_{ij}\left\{\beta_{ij} - \log \left[\sum_j \exp(\beta_{ij})\right]\right\} - \sum_i \frac{1}{2} \log \left[\sum_j \exp(\beta_{ij})\right]^2 \Big/ \sigma^2 - m \log \sigma.$$

At this stage the $nr+n$ quantities P_{ij}, C_i have been replaced by the nr quantities β_{ij}, and the constraints 1.2 have been eliminated.

In order to eliminate the constraints 1.8, note that it is possible to express any β_{ij} in terms of any other β_{ij} and the Φ_{ij} lying on the same downward sloping diagonal. For example,

$$\beta_{33} = \beta_{11} + \gamma_1 - \gamma_3 - \Phi_{11} - \Phi_{22}.$$

Because there are $n+r-1$ downward sloping diagonals, all the β_{ij} can be expressed in terms of $n+r-1$ of them, the fundamental betas. To decide which betas to use as the fundamental ones, consider the following discussion. When deciding which parameters to employ for parameterizing the likelihood function in a nonlinear parameter estimation problem, it is desirable to employ those parameters which are best determined by the problem and have small covariance with other parameters. The β_{ij} which are best determined are those corresponding to values of i and j for which C_{ij} forms a large proportion of the catch in that year. This will in general occur for a value of j lying about halfway between 1 and r.

Let m be the greatest integer less than or equal to $r/2$. The fundamental betas which have been used are $\beta_{n1}, \beta_{n2}, \ldots, \beta_{nm}, \beta_{n-1,\, m}, \ldots, \beta_{1m}, \ldots, \beta_{1r}$.

The problem has now been reformulated as an unconstrained maximization involving the $n+r-1$ fundamental betas and the $(n-1)(r-1)$ quantities Φ_{ij}.

2. Reparameterizing the Instantaneous Mortalities

In section 2 the problem of reparameterizing the instantaneous fishing and natural mortality rates is considered. The purpose of this reparameterization is to enable us to use the model to determine the most regular analysis of the history of the fishery which is consistent with the catch at age data, whereby regular is meant that analysis of the fishery in which the estimates of fishing and natural mortality vary in the simplest biologically meaningful manner.

Up to now the problem has not been solved; it has merely been restated. This is because the $(n-1)(r-1)$ quantities Φ_{ij} depend on $2nr$ quantities, the F_{ij} and M_{ij}, so that the problem now depends on $n+r-1+2nr$ quantities; whereas originally we had just the $nr+r$ quantities P_{ij} and C_i.

The reason why some progress has been made is that the instantaneous mortality rates can be reparameterized to exploit underlying regularities in the process being studied. For example, one can assume, as is often done, that the instantaneous natural mortality rate is independent of year class and fishing year. Then $M_{ij} = M$ and the number of instantaneous natural mortality quantities has been reduced from nr to 1. More complicated schemes of parameterizing the instantaneous natural mortality are possible. For example, one could assume that the instantaneous natural mortality is a linear function of age class so that

$$M_{ij} = a + bj.$$

In the situations studied to date it was discovered that instantaneous natural mortality was not determined sufficiently well to justify attempts to determine age-dependent effects, and age-independent natural mortality has been used throughout. Further research should be done in order to determine whether there are conditions under which finer estimates of natural mortality can be obtained.

The possibilities for parameterizing instantaneous fishing mortality are considerably more varied. In order to get a general idea of how to proceed, we consider that fishing mortality depends on the interaction of two systems, fishermen and fish. If the fishermen do not fish, the fishing mortality will be zero, no matter what the fish do. On the other hand, if a particular year class is too small to be caught, or is in another area, its fishing mortality will be zero no matter what the fishermen do. With these ideas in mind Doubleday (1976) employed a two-factor model $\log (F_{ij}) = a_i + b_j$, where a_i represents a general level of fishing mortality due to the fishermen, and b_j represents the relative level of fishing vulnerability of year class j.

We use here a different approach to parameterizing the instantaneous fishing mortality in addition to Doubleday's method. It was hypothesized that the fishing vulnerability should follow an age-dependent trend and should therefore be estimated by a curve depending on a smaller number of parameters than the number of age classes.

As a first attempt to reparameterize the fishing mortality rate, a parabola was employed. This had the disadvantage that if the fishing vulnerability increased very quickly at the beginning, it must at some point decrease very quickly. To overcome this difficulty we employed a nonlinear rescaling of the j index. The expression for the fishing mortality curve is

$$2.1 \qquad \log F_{ij} = b_1 j(s) + b_2 j(s)^2 + a_i$$

where the method for rescaling the j index is given by

$$2.2 \qquad j(s) = -1 + 2\,(1 - s^{j-1})/(1 - s^{r-1})$$

with $0 < s < 1$, hereafter referred to as the VB parameterization.

3. The Incorporation of Fishing Effort

In many situations one has not only catch at age information for a fishery but also estimates of fishing effort. There are three reasons for including such information into the model. First, if there is a relationship between fishing effort and fishing mortality which can be modeled, then the time series of effort contains extra information which can be used to improve the estimates of whatever it is one wants to know. Such information improves the estimate of natural mortality. Second, it may be desirable to estimate the relationship, if any, between fishing effort and fishing mortality in order to determine what desirable levels of fishing effort are. In particular it is possible to examine the data for evidence of time-dependent trends in catchability. Finally, if the last year class is not fished out, such information improves estimates of the number of survivors.

In this model it has been assumed that for a given year the average level of instantaneous fishing mortality is related to effort. More precisely, let E_i be the total fishing effort in year i. It is assumed that

$$3.1 \qquad \log F_{ij} = b_{ij} + \log(q_i) + \log(E_i) + D_i$$

where $b_{ij} = b_1 j(s) + b_2 j(s)^2$
where in equation 3.1 D_i represents the deviation from the general level of fishing mortality for the year i.

The quantities D_i are assumed to be normally distributed random variables with mean 0 and variance σ_1^2. Thus the sum $\sum_i D_i^2/2\sigma_1^2$ is subtracted from the log-likelihood function.

4. The Problem of Relative Error Sizes

Section 4 treats the problem of estimating the relative magnitude of the errors present in the various types of information used by the model.

As we already stated, a stochastic model should attempt to allocate errors in a reasonable fashion. In this regard consider the assumption that the S_{ij} are obtained by aging a random sample of the catch. Now in most cases the sampling of the catch is almost certainly not random. For example, it is in general not possible to sample the catches from all boats, and in many fisheries the age structure of the catch may differ substantially from boat to boat and season to season. Other problems arise in sampling the catch from a particular boat. At this point then the reader may well wonder about the wisdom of assuming a random sampling scheme in the model. The answer is twofold. First the assumption of a random sample is akin to the assumption of normality made in many situations in that it is in some sense the simplest assumption to make in the absence of further information. To understand the second reason for the suitability of this assumption, consider a random sample of 400 fish from a population which consists of 20% 5-yr-old fish and 1% 10-yr-old fish. The expected numbers of 5- and 10-yr-old fish are 80 and 4 fish. Now an actual turnout of 6 age 10 fish would not be surprising; however, an actual turnout of 120 age 5 fish would be highly unusual. In both cases the percentage error is 50%. Thus the percentage error in estimating a population percentage gets large as the population percentage gets small.

Let p be the true population percentage and $\hat{p}$ be an estimate of p derived from taking a random sample of size m. The variance of $\hat{p}$ is $p(1 - p)/m$, and the variance of $\hat{p}/p$ is $(1 - p)/pm$, which becomes unbounded as p tends to zero.

This seems to be a fundamental property of sampling errors which should hold even when the sampling is not truly random. The adoption of the random sample hypothesis and the use of the corresponding likelihood function ensures that these relative error size probabilities will be respected when the model attempts to fit the data.

Another question raised by these considerations is the problem of sample size. Because of the unknown errors involved it is probably not true that a sample 25 times as large yields 5 times more accurate estimates, which is what sampling theory would predict if the samples were random.

For this reason the sample sizes have been scaled so that they are all equal to 400. This means approximately that if a true population percentage is 0.2, then the observed value would lie between 0.16 and 0.24 96% of the time. Of course if it is known that the age structure data for certain years is bad, the sample sizes for these years can be set correspondingly lower.

Because the age sample sizes have been fixed in a somewhat arbitrary fashion, it was not considered necessary to estimate σ^2, and σ^2 was set to be equal to 0.0025. This corresponds to approximately a 5% average error in estimating the total number of fish caught.

The question of determining the size of σ_1^2 is of a different nature than the determination of stock size and σ^2. This is because one must assume that the age structure and total catch information are relatively accurate, because if it is not, then there is no information, and hence no basis on which to do any analysis. An appropriate procedure is to start with a small value of σ_1^2, observe the resulting relationships, and then increase σ_1^2 if this seems necessary to get a better fit between predicted and observed age structure and total catch data. The effects of this procedure on the original solution can be observed and the appropriate conclusions drawn.

Thus σ^2 and $\sigma_1{}^2$ are not regarded as quantities to be estimated but are held at fixed values. Let $w = 1/\sigma^2$ and $w_1 = 1/\sigma_1{}^2$. With this provision the log-likelihood function is given by

$$4.1 \qquad \sum_{i,j} S_{ij}\left\{\beta_{ij} - \left[\log \sum_j \exp(\beta_{ij})\right]\right\} - w \sum_i \frac{1}{2}\log\left[\sum_j \exp(\beta_{ij})\right]^2 - w_1 \sum_i \frac{1}{2} D_i^2.$$

The quantities w and w_1 can be thought of as penalty weights which determine what penalty must be paid for deviating from the observed total catch or the effort-fishing mortality relationship.

These procedures for adjusting the various variances until a suitable fit is deemed to be achieved may seem somewhat arbitrary to the reader, and they are. It is simply an inescapable fact that the age structure and effort data do not contain enough information to determine the relative accuracies of the aging data, the total catch data, the regularity of fishing mortality, or the closeness of the relationship between effort and average fishing mortality. These procedures do, however, give the user a precise quantitative method of exploring the results of various assumptions about the relative error sizes involved.

5. Factors Affecting Recruitment

A serious deficiency in the model as it now stands is its inability to predict what will occur in the fishery in the future. This is because there is no mechanism for predicting future recruitment. If there were such a mechanism, then because there are already estimates of the relationship between fishing effort and fishing mortality, it would be possible to construct scenarios describing the future behavior of the stock under various management strategies.

There are two obvious factors which may affect recruitment: parent stock size and the environment. The environment is of course a catch-all phrase for a host of factors. Whereas environmental factors may be very important in determining recruitment, recruitment relationships based primarily on environmental factors may not be of much value for predicting future stock behavior, as the future value of the factors may be essentially unknowable.

On the other hand knowledge of environmental factors affecting recruitment may be of great importance in order to have the greatest possible lead time for predicting serious recruitment failures so that appropriate action can be taken.

In this section we consider the effects of stock size only on recruitment.

There are many aspects of parent stock condition which may have a bearing on the resulting recruitment. For simplicity we consider only a simple situation. We assume that the recruitment depends on the reproductive potential of the female members of the stock and we have used the "Ricker curve" for the relationship. The reader who does not believe in this form of stock–recruitment relationship should be reassured that it is used only for illustrative purposes and that any other desired relationship could easily be substituted.

Let f_j denote the relative reproductive potential of age class j fish (The f_j could be made time dependent if the information were available and if that were deemed advisable.)

Suppose that the age of recruitment is a. The reproductive potential of P_i of the population in year i is given by

$$5.1 \qquad P_i = \sum_j f_j N_{ij}.$$

The stock–recruitment relationship is assumed to have the form

$$5.2 \qquad N_{i+a,\,1} = \alpha P_i \exp(-\delta P_i)\, e^{\epsilon_i}$$

where the ϵ_i are normally distributed random variables with mean 0 and variance $\sigma_2{}^2$. The contribution to the log-likelihood function from the stock–recruitment relationship is

$$5.3 \qquad -\sum_{i=1}^{n-a} \frac{1}{2}(\log\,(N_{i+a,1}/P_i) - \log\alpha + \delta P_i)^2/\sigma_2{}^2.$$

Because the f_j are constants and equation 1.3 can be used to eliminate the N_{ij}, only two new parameters are introduced into the model. ($\sigma_2{}^2$ is treated as a constant as discussed in the section on the Problem of Relative Error Sizes.)

6. Errors in Aging

The problem posed by small aging errors in applying the model to certain fish populations cannot be overemphasized. Such populations are those where recruitment varies widely from year to year. To see why this is so, consider an aging procedure which is accurate for the first age class and suppose that for age classes 4, 5, and 6 the procedure gives the correct age 80% of the time and is either one year high or low 10% of the time. Suppose that age classes 4 and 6 are from large cohorts and age class 5 is from a small cohort so that the true age structure of the catch is 60% fours, 5% fives, and 20% sixes. Then with the above assumptions about the aging errors it is easily seen that the expected percentage of age class 5 fish observed will be 12% which would be a 140% error.

When a small cohort is followed through the fishery it would be observed to have abnormally low fishing mortality at the beginning and abnormally high fishing mortality at the end with the result that the true regularities in fishing mortality, whose existence the model is trying to exploit, would be masked. In addition, interpretation of model fit is made more difficult.

Another problem caused by small aging errors is that very large recruitments appear smaller and, (perhaps more serious) very small recruitments appear larger. This effect will make the identification of environmental factors affecting recruitment, especially those leading to catastrophic recruitment failures, more difficult.

A great advantage of this model is the simplicity with which aging error information can be incorporated into it.

Let a_{jk} be the probability that a fish from age class k will be judged to lie in age class j.

The probability that a fish picked at random in year i will be judged to lie in age class j is given by

$$6.1 \qquad \sum_k a_{jk} P_{ik}.$$

The first terms in the log-likelihood function become

$$6.2 \qquad \sum_{i,j} S_{ij} \log \left(\sum_k a_{jk} P_{ik} \right)$$

while the other terms are unaffected. Because

$$P_{ik} = \exp(\beta_{ik}) \Big/ \sum_l \exp(\beta_{il})$$

the log-likelihood function becomes

$$6.3. \qquad \sum_{i,j} S_{ij} \log \left\{ \sum_k a_{jk} \left[\exp(\beta_{ik}) \Big/ \sum_l \exp(\beta_{il}) \right] \right\}$$

$$- \sum_i \frac{1}{2} \left[\sum_j \exp(\beta_{ij}) \right]^2 \Big/ \sigma^2$$

where the log-likelihood contributions from the fishing effort information and stock–recruitment relationship etc. have been omitted.

7. Grouping the Aging Data for the Older Age Classes

Some species of fish may have so many age classes present in a fishery that it is desirable to group the aging data for older age classes together rather than consider them separately. Aging the older fish may be very time consuming, and in addition the estimates of the ages of the older fish may be so inaccurate that including them will actually degrade the performance of the model. The grouping of the aging data for the older age classes can be accomplished by a simple modification of the likelihood function.

Suppose that the aging data for all fish lying in age classes s to r inclusively are to be grouped. Let

$$7.1 \qquad T_i = \sum_{j=s}^{r} S_{ij}.$$

The first part of the log-likelihood function (1.1) becomes

$$7.2 \qquad \sum_{i=1}^{n} \sum_{j=1}^{s-1} S_{ij} \log (P_{ij}) + \sum_{i=1}^{n} T_i \left[\log \left(\sum_{k=s}^{r} P_{ik} \right) \right].$$

8. An Example

To illustrate how various aspects of the model function in practice, we simulated an exploited fish population and analyzed the resulting observations using the model. The results are presented here.

The population simulated had a natural mortality rate of 0.5, and a Ricker type of stock–recruitment relationship (expression 5.2) with alpha = 9.0, delta = 0.006, and a variance $\sigma_2^2 = 0.09$.

TABLE 1. The actual number of fish at age.

	Age									
Year	4	5	6	7	8	9	10	11	12	13
1	400	1000	600	200	300	50	10	20	5	2
2	1000	236	556	304	91	125	19	4	7	2
3	700	595	135	297	151	43	55	8	2	3
4	300	416	339	72	148	70	19	24	3	1
5	67	172	212	143	25	42	17	4	5	1
6	97	39	89	92	51	7	11	4	1	1
7	118	54	17	29	21	9	1	1	0	0
8	241	70	31	9	14	10	4	0	1	0
9	1007	144	40	17	5	7	5	2	0	0
10	301	596	81	21	8	2	3	2	1	0
11	478	169	281	29	6	2	0	0	0	0
12	470	273	84	113	9	1	0	0	0	0
13	378	280	157	46	58	4	1	0	0	0
14	917	207	122	48	9	8	0	0	0	0
15	357	512	96	43	12	2	1	0	0	0
16	861	211	289	50	20	5	1	1	0	0
17	738	512	120	153	25	9	2	0	0	0
18	629	429	271	55	60	8	3	1	0	0
19	465	364	225	122	21	19	2	1	0	0
20	463	276	206	118	59	9	8	1	0	0

TABLE 2. The catch at age.

Year	Age 4	5	6	7	8	9	10	11	12	13
1	8	66	78	39	75	14	3	7	2	1
2	15	11	52	44	17	27	5	1	2	0
3	10	28	13	43	28	9	13	2	0	1
4	13	53	83	25	64	34	10	13	2	0
5	3	20	48	47	10	19	8	2	3	0
6	7	8	33	47	31	5	8	3	1	1
7	2	3	2	4	4	2	0	0	0	0
8	3	3	2	1	2	2	1	0	0	0
9	19	8	5	3	1	2	1	1	0	0
10	18	106	27	10	4	1	2	1	0	0
11	23	24	76	11	3	1	0	0	0	0
12	6	11	7	14	1	0	0	0	0	0
13	30	63	63	25	37	3	0	0	0	0
14	57	38	41	22	5	5	0	0	0	0
15	6	29	11	7	3	0	0	0	0	0
16	14	11	29	8	4	1	0	0	0	0
17	24	51	23	43	9	4	1	0	0	0
18	22	46	56	17	23	4	1	0	0	0
19	8	19	24	20	4	5	1	0	0	0
20	11	21	31	26	17	3	3	0	0	0

TABLE 3. The aging error probabilities.

True age	Underage by 1 yr	Correct age	Overage by 1 yr
4	0.00	0.80	0.20
5	0.10	0.70	0.20
6	0.10	0.65	0.25
7	0.20	0.60	0.20
8	0.25	0.55	0.20
9	0.30	0.50	0.20
10	0.40	0.40	0.20
11	0.40	0.40	0.20
12	0.50	0.40	0.10
13	0.50	0.50	0.00

The fishing mortality was generated according to the VB parameterization described by expression 3.1 with deviations from average fishing mortality having a variance $\sigma_1^2 = 0.09$. The actual fishing mortality is given in Table 5.

The population, catch, and observed age structure of the catch were generated by stochastic simulation. The stochastic element consists of three parts, the stochastic error in the effort-fishing mortality relationship, the stochastic error in the stock−recruitment relationship, and the sampling error in sampling the catch for fish to age. For each year a random sample of 400 fish was generated from the catch and aged according to the aging error probabilities shown in Table 3.

The analysis has been split up into four sets of computer runs of the model. The first set investigates the performance

TABLE 4. The observed numbers at age in the aging samples (from aging 400 fish with aging error probabilities given in Table 3).

Year	Age 4	5	6	7	8	9	10	11	12	13
1	16	77	113	83	60	33	10	6	2	0
2	28	38	103	108	52	46	17	4	3	1
3	31	68	58	98	63	47	23	10	2	0
4	27	65	80	70	82	40	19	14	3	0
5	11	50	114	96	51	40	26	6	4	2
6	16	24	116	130	70	26	10	7	1	0
7	41	60	61	102	71	40	20	2	3	0
8	73	83	54	53	57	47	13	13	6	1
9	153	127	52	27	15	12	12	2	0	0
10	57	187	87	34	16	9	4	5	1	0
11	61	77	171	74	11	2	1	2	1	0
12	69	84	110	86	41	8	1	0	0	1
13	46	102	105	74	51	22	0	0	0	0
14	117	97	86	66	18	8	8	0	0	0
15	61	152	101	66	16	4	0	0	0	0
16	78	83	124	64	32	12	5	2	0	0
17	56	109	101	91	32	7	4	0	0	0
18	55	96	118	71	31	24	4	1	0	0
19	28	88	117	101	43	14	7	2	0	0
20	38	84	99	96	50	24	4	4	1	0

TABLE 5. The actual fishing mortality.

The relative fishing vulnerability

0.050	0.159	0.329	0.517	0.686	0.816	0.906	0.964	1.000	1.000

The instantaneous fishing mortality

Year	Age 4	5	6	7	8	9	10	11	12	13
1	0.03	0.09	0.18	0.28	0.37	0.45	0.49	0.53	0.55	0.55
2	0.02	0.06	0.13	0.20	0.26	0.31	0.35	0.37	0.38	0.38
3	0.02	0.06	0.13	0.20	0.26	0.31	0.35	0.37	0.39	0.39
4	0.06	0.18	0.36	0.57	0.76	0.90	1.00	1.07	1.11	1.11
5	0.05	0.16	0.33	0.52	0.69	0.82	0.91	0.97	1.01	1.01
6	0.09	0.30	0.62	0.98	1.29	1.54	1.71	1.82	1.89	1.89
7	0.02	0.06	0.13	0.20	0.26	0.31	0.35	0.37	0.39	0.39
8	0.02	0.05	0.10	0.16	0.21	0.25	0.28	0.29	0.30	0.30
9	0.02	0.08	0.16	0.25	0.33	0.40	0.44	0.47	0.49	0.49
10	0.08	0.25	0.52	0.83	1.10	1.30	1.45	1.54	1.60	1.60
11	0.06	0.20	0.41	0.65	0.86	1.03	1.14	1.21	1.26	1.26
12	0.02	0.05	0.11	0.17	0.22	0.26	0.29	0.31	0.32	0.32
13	0.10	0.33	0.69	1.08	1.44	1.71	1.90	2.02	2.10	2.10
14	0.08	0.26	0.54	0.86	1.14	1.35	1.50	1.60	1.66	1.66
15	0.02	0.07	0.15	0.24	0.32	0.38	0.42	0.45	0.47	0.47
16	0.02	0.07	0.14	0.21	0.28	0.34	0.38	0.40	0.41	0.41
17	0.04	0.13	0.28	0.44	0.58	0.69	0.77	0.82	0.85	0.85
18	0.05	0.15	0.30	0.48	0.63	0.75	0.83	0.89	0.92	0.92
19	0.02	0.07	0.14	0.23	0.30	0.36	0.40	0.42	0.44	0.44
20	0.03	0.10	0.21	0.33	0.44	0.52	0.58	0.61	0.64	0.64

The actual effort

2	1	1	5	4	5	1	1	2	5
4	1	5	3	1	1	3	2	2	2

The deviations in the effort-fishing mortality relationship

−0.23	0.11	0.11	−0.44	−0.31	0.09	0.11	−0.12	−0.35	−0.08
−0.09	−0.07	0.20	0.47	0.30	0.19	−0.20	0.29	−0.46	−0.08

TABLE 6. The stock–recruitment relationship.

The coefficients for the Ricker curve

$\alpha = 9.0$ $\delta = 0.006$

The age of recruitment is 4.

The relative reproductive potentials

0.10	0.20	0.30	0.50	0.70	0.90	1.00	1.00	1.00	1.00

The maximum reproduction is at 0.57 times the average reproductive potential of 295.

The reproductive potentials (for years 1–16)

812	674	590	464	258	150	67	75	166	197
186	191	209	208	200	260				

The predicted recruitment (without stochastic error for years 5–20))

55	105	153	257	493	549	404	432	551	543
548	546	536	537	542	491				

The stochastic error in the stock–recruitment relationship

0.177	−0.086	−0.268	−0.066	0.713	−0.600	0.167	0.082	−0.378	0.523
−0.429	0.455	0.319	0.158	−0.152	−0.059				

SET 1: This set of runs represents the best analysis of the population which could be obtained from the data. In particular, it is assumed that the aging error probabilities are known and have been supplied to the model. The results from set 1 are summarized in Tables 7 through 10.

TABLE 7. Value of the objective function for different values of the instantaneous natural mortality M.

M	0.3	0.4	0.5	0.6	0.7
Objective function	85.6	84.6	84.2	84.3	85.0

TABLE 8. The estimated number of fish at age.

	Age									
Year	4	5	6	7	8	9	10	11	12	13
1	365	1024	602	216	227	86	7	4	10	0
2	937	215	567	303	98	94	33	2	1	3
3	647	557	122	302	151	46	41	14	1	1
4	382	384	317	65	149	70	20	17	6	0
5	52	219	193	131	22	41	16	4	3	1
6	97	30	112	83	46	6	11	4	1	1
7	123	53	13	36	19	8	1	1	0	0
8	275	73	30	7	18	9	3	0	0	0
9	1006	165	42	17	4	9	4	2	0	0
10	322	596	93	22	8	2	4	2	1	0
11	456	181	284	35	6	2	0	1	0	0
12	514	260	90	116	11	2	0	0	0	0
13	359	307	150	50	60	6	1	0	0	0
14	845	197	135	47	11	9	1	0	0	0
15	410	472	91	48	12	2	2	0	0	0
16	855	243	266	48	23	5	1	1	0	0
17	649	508	138	141	23	10	2	0	0	0
18	575	377	268	63	55	8	3	1	0	0
19	408	332	196	119	23	17	2	1	0	0
20	418	242	187	102	56	10	7	1	0	0

TABLE 9. Estimates associated with the stock–recruitment relationship for Set 1 with $M = 0.5$.

The estimated coefficients for the Ricker curve

$\alpha = 9.84$ $\delta = 0.0064$

The estimated maximum reproduction is at 0.54 times the estimated average reproductive potential of 290.

The predicted recruitment (for years 5–20)

52	101	151	249	501	567	434	474	567	548
557	552	538	548	552	489				

The estimated residuals for the stock–recruitment

0.02	−0.04	−0.21	0.10	0.70	−0.57	0.05	0.08	−0.46	0.43
−0.31	0.44	0.19	0.05	−0.30	−0.16				

The correlation between the estimated and actual deviations from the stock–recruitment relationship is 0.96.

of the model when it is given the correct aging error probabilities. The second set investigates its performance when it is assumed that there are no aging errors. The third set investigates the effect of grouping the last age classes together. For all three sets the relative reproductive potentials have been assumed known and have been supplied to the model. The first three sets all use the VB parameterization of the fishing mortality. The fourth set is the same as the third except that the Doubleday parameterization of the fishing mortality has been used instead of the VB parameterization.

For all runs, the penalty weights for the stock–recruitment relationship and the deviations from average fishing mortality have been set equal to 2.

The relevant aspects of the simulated fish population are

TABLE 10. The estimated fishing mortality.

The estimated relative fishing vulnerability

0.047	0.149	0.302	0.470	0.623	0.748	0.844	0.914	0.965	1.000

The estimates of instantaneous fishing mortality

Year	Age 4	5	6	7	8	9	10	11	12	13
1	0.03	0.09	0.19	0.29	0.38	0.46	0.51	0.56	0.59	0.61
2	0.02	0.06	0.13	0.20	0.27	0.32	0.36	0.39	0.41	0.43
3	0.02	0.06	0.13	0.20	0.27	0.32	0.37	0.40	0.42	0.44
4	0.06	0.19	0.38	0.59	0.78	0.94	1.06	1.15	1.21	1.26
5	0.05	0.17	0.35	0.54	0.71	0.86	0.97	1.05	1.11	1.15
6	0.10	0.31	0.63	0.97	1.29	1.54	1.74	1.89	1.99	2.07
7	0.02	0.06	0.12	0.19	0.25	0.30	0.34	0.37	0.39	0.40
8	0.01	0.05	0.09	0.14	0.19	0.22	0.25	0.27	0.29	0.30
9	0.02	0.07	0.15	0.23	0.30	0.37	0.41	0.45	0.47	0.49
10	0.08	0.24	0.49	0.76	1.01	1.21	1.36	1.48	1.56	1.62
11	0.06	0.19	0.40	0.61	0.81	0.98	1.10	1.20	1.26	1.31
12	0.01	0.05	0.10	0.16	0.20	0.25	0.28	0.30	0.32	0.33
13	0.10	0.32	0.66	1.02	1.36	1.63	1.84	1.99	2.10	2.17
14	0.08	0.27	0.54	0.84	1.11	1.34	1.51	1.63	1.72	1.78
15	0.02	0.07	0.15	0.23	0.31	0.37	0.42	0.46	0.48	0.50
16	0.02	0.07	0.14	0.21	0.28	0.33	0.38	0.41	0.43	0.45
17	0.04	0.14	0.28	0.44	0.58	0.70	0.79	0.86	0.90	0.94
18	0.05	0.16	0.32	0.49	0.65	0.78	0.88	0.95	1.01	1.04
19	0.02	0.08	0.16	0.24	0.32	0.39	0.44	0.47	0.50	0.52
20	0.04	0.12	0.23	0.36	0.48	0.58	0.65	0.71	0.75	0.77

The estimated residuals for the effort-fishing mortality relationship

−0.17	0.17	0.18	−0.37	−0.23	0.13	0.10	−0.19	−0.40	−0.11
−0.10	−0.09	0.18	0.50	0.32	0.21	−0.15	0.37	−0.34	0.06

The correlation between the estimated and actual deviations from the effort-fishing mortality relationship is 0.98.

SET 2: Set 2 is the same as Set 1 except that the model is run under the assumption that there are no aging errors. The results from set 2 are summarized in Tables 11 through 14.

TABLE 11. Value of the objective function for different values of the instantaneous natural mortality M.

M	0.5	0.6	0.7	0.8	0.9	1.0
Objective function	131.6	130.3	129.5	129.4	129.8	130.7

summarized in Tables 1 through 6.

The goodness of fit for the various runs is measured by the log-likelihood function with its sign changed. Thus a smaller value of the objective function denotes a better fit to the observed data.

Summary and Conclusions

We deal first with the results from set 4. Examining the estimated relative fishing vulnerability in Table 19, it is clear that the parameter estimates have become unstable. There is simply not enough information to determine them when the older age classes are grouped together, and a more restrictive parameterization must be used.

We emphasize that we in no way wish to imply that the Doubleday parameterization is of no value. In other situations, the Doubleday, VB, or indeed some other parameterization of the fishing mortality could be the appropriate one.

In evaluating the performance of the model for the other three sets, we shall concentrate on three aspects of the analysis. These are the ability of the model to estimate the instantaneous natural mortality rate M, the ability of the model to synthesize the stock−recruitment relationship, and the ability of the model to detect deviations from average fishing mortality. For comparing the latter two attributes the instantaneous natural mortality rate has been fixed at 0.5 for all three

TABLE 12. The estimated numbers of fish in the population for set 2 with $M = 0.5$.

	Age									
Year	4	5	6	7	8	9	10	11	12	13
1	773	853	594	295	190	79	19	10	3	0
2	814	456	475	301	134	78	30	7	3	1
3	677	484	261	255	150	62	34	12	3	1
4	349	403	277	140	127	69	27	14	5	1
5	120	200	206	118	48	35	16	6	3	1
6	114	69	105	91	43	14	9	4	1	1
7	172	63	33	37	23	8	2	1	0	0
8	439	103	37	18	19	11	4	1	0	0
9	828	264	61	21	10	10	6	2	0	0
10	468	492	151	32	10	5	4	2	1	0
11	484	265	243	59	10	2	1	1	0	0
12	511	278	136	104	20	3	1	0	0	0
13	506	306	162	76	55	10	1	0	0	0
14	738	282	142	56	18	10	1	0	0	0
15	603	416	136	54	16	4	2	0	0	0
16	810	358	237	72	26	7	2	1	0	0
17	728	482	205	127	36	12	3	1	0	0
18	616	425	259	97	51	13	4	1	0	0
19	483	358	225	119	37	17	4	1	0	0
20	454	287	203	119	58	17	7	1	0	0

TABLE 13. Estimates associated with the stock–recruitment relationship for set 2 with $M = 0.5$.

The estimated coefficients for the Ricker curve
$\alpha = 9.05$ $\delta = 0.0054$

The estimated maximum reproduction is at 0.59 times the estimated average reproductive potential of 311.

The predicted recruitment (for years 5–20)

92	162	227	339	574	610	487	557	616	603
609	608	588	604	602	551				

The estimated residuals for the stock–recruitment

0.27	−0.35	−0.28	0.26	0.37	−0.26	−0.01	−0.09	−0.20	0.20
−0.01	0.29	0.21	0.02	−0.22	−0.19				

The correlation between the estimated and actual deviations from the stock–recruitment relationship is 0.76.

TABLE 14. The estimated fishing mortality.

The estimated relative fishing vulnerability

0.043	0.133	0.281	0.455	0.619	0.754	0.853	0.923	0.969	1.000

The estimated residuals for the effort-fishing mortality relationship

−0.08	0.25	0.25	−0.31	−0.19	0.11	−0.04	−0.42	−0.44	−0.10
−0.09	−0.09	0.16	0.50	0.32	0.22	−0.13	0.38	−0.34	0.04

The correlation between the estimated and actual deviations from the effort-fishing mortality relationship is 0.91

sets in order to make it easier to compare the resulting parameter estimates.

The performance of the model in estimating the instantaneous natural mortality rate is presented in Tables 7, 11, and 15.

Set 1 (Tables 7–10) has the best result with the minimum of the objective function occurring near its true value of 0.5. Set 2 (Tables 11–14) gives the worst result with the minimum occurring near 0.8. This indicates a strong sensitivity of the estimate of this parameter to the existence of the aging

SET 3: For the runs in set 3 the last seven age classes in the input data were grouped together and the model is run under the assumption that there are no aging errors. The results from set 3 are summarized in Tables 15 through 18.

TABLE 15. Value of the objective function for different values of the instantaneous natural mortality M.

M	0.3	0.4	0.5	0.6	0.7
Objective function	25.1	24.7	24.9	25.5	26.3

TABLE 16. The estimated numbers of fish in the population for set 3 with $M = 0.5$.

	Age									
Year	4	5	6	7	8	9	10	11	12	13
1	423	1039	727	3	585	2	1	11	13	0
2	935	250	579	371	1	264	1	1	5	6
3	680	557	143	310	189	1	127	0	0	2
4	344	405	317	76	156	92	0	60	0	0
5	75	197	204	132	27	50	28	0	17	0
6	90	43	101	88	49	9	16	9	0	5
7	125	50	20	34	23	11	2	3	2	0
8	271	75	29	11	17	11	5	1	1	1
9	1065	162	43	16	6	9	6	3	0	1
10	345	632	91	23	8	3	4	3	1	0
11	487	195	303	35	7	2	1	1	1	0
12	519	279	98	127	12	2	1	0	0	0
13	412	310	162	54	67	6	1	0	0	0
14	986	228	139	53	14	14	1	0	0	0
15	437	557	110	52	16	4	4	0	0	0
16	930	260	317	58	26	8	2	2	0	0
17	755	554	148	171	30	13	4	1	1	0
18	629	441	297	70	72	12	5	1	0	0
19	478	366	233	136	28	27	4	2	0	0
20	453	284	207	123	68	14	13	2	1	0

TABLE 17. Estimates associated with the stock–recruitment relationship for Set 3 with $M = 0.5$.

The estimated coefficients for the Ricker curve
$\alpha = 9.237$ $\delta = 0.5524E\text{-}02$

The estimation maximum reproduction is at 0.55 times the estimated average reproductive potential of 326.

The predicted recruitment (for years 5–20)

56	109	172	291	548	613	465	495	615	605
610	607	594	592	594	530				

The estimated residuals for the stock–recruitment are

0.29	−0.18	−0.32	0.07	0.66	−0.57	0.05	0.05	−0.40	0.49
−0.33	0.43	0.24	0.06	−0.22	−0.16				

The correlation between the estimated and actual deviations from the stock–recruitment relationship is 0.98.

errors if they are not accounted for.

Set 3 (Tables 15–18) gives a good result with an estimate of M near 0.4.

The fact that the objective function decreased from 129.4 to 84.2 when the correct aging error probabilities were incorporated into the model indicates that at least in some cases it might be possible to use the model to estimate the aging error probabilities. On the other hand the fact that M was estimated better in set 3 than in set 2 indicates that if the aging error probabilities are unknown or cannot be estimated for the older fish, then it is better to use only the age structures for the younger fish which are aged almost without error and to group the older fish together.

The performance of the model in synthesizing the stock–

TABLE 18. The estimated fishing mortality.

The estimated relative fishing vulnerability									
0.074	0.245	0.496	0.714	0.853	0.929	0.968	0.987	0.996	1.000
The estimated residuals for the effort-fishing mortality relationship									
−0.179	0.184	0.232	−0.314	−0.200	0.154	0.142	−0.121	−0.335	−0.079
−0.098	−0.070	0.178	0.430	0.241	0.151	−0.197	0.302	−0.404	0.002

The correlation between the estimated and actual deviations from the effort-fishing mortality relationship is 0.98.

SET 4: Set 4 is identical to set 3 except that the Doubleday parameterization of the fishing mortality has been used instead of the VB parameterization. The results for set 4 are given in Table 19.

TABLE 19. The estimated relative fishing vulnerability.

0.084	0.251	0.519	0.734	1.000	0.389	0.884	0.844	0.069	0.002

recruitment relationship is presented in Tables 9, 13, and 17. The correct parameters of the stock–recruitment relationship are presented in Table 6.

In all three sets the model was able to identify with good accuracy the relationship between the maximum reproduction and the estimated average reproductive potential. This is important because it is this information which indicates whether heavier exploitation will result in an increase or decrease in the expected recruitment.

Another point to be considered when examining the stock–recruitment relationship is the ability of the model to estimate correctly the residuals. They are important because if environmental factors affecting the recruitment process are to be detected, it is necessary for the model to estimate the residuals well.

In set 1 the correlation between the actual and estimated residuals was 0.96. In sets 2 and 3 it was 0.76 and 0.98, respectively. Thus the effect of not accounting for the aging errors was to reduce to a considerable degree the ability of the model to estimate these residuals, and it is again demonstrated that for some quantities the estimates are better if the older ages are grouped if the aging errors are not to be taken into account.

The effect of the aging errors can be seen clearly by comparing Tables 1 and 12 for the estimated number of 4-yr-old fish in the population, where it can be seen that they produce a characteristic smoothing of these estimates.

The deviations from average fishing mortality are important because they must be well estimated to detect such phenomena as variations in fleet efficiency or catchability.

The actual deviations from average fishing mortality are given in Table 5. The estimated deviations from average fishing mortality are given in Tables 10, 14, and 18. For the three sets the respective correlations were 0.98, 0.91, and 0.98. Thus once again grouping the ages together gives better results than ignoring the aging errors.

One point has been made. The process of aging fish to obtain information about the age structure of the catch is expensive and time consuming. This data should not be produced without considering the final use to which it will be put. If this final use is an age-structured model, then aging a large number of older fish "almost" accurately, although a triumph of laboratory procedure, may not only be a waste of money and effort, but may actually degrade the quality of the estimates obtained from the age-structured model.

DOUBLEDAY, W. G. 1976. A least square approach to analyzing catch at age data. Int. Comm. Northwest Atl. Fish. Res. Bull. 12: 69–81.

FRY, F. E. J. 1949. Statistics of a lake trout fishery. Biometrics 5: 26–27.

GULLAND, J. A. 1965. Estimation of mortality rates. Annex to Arctic fisheries working group report. I.C.E.S., C.M. Doc. No. 3. (Mimeogr.)

JONES, R. 1964. Estimating population size from commercial statistics when fishing mortality varies with age. Rapp. Cons. Explor. Mer 155(38): 210–214.

PALOHEIMO, J. E. 1980. Estimating mortality rates in fish populations. Trans. Am. Fish. Soc. 109: 378–386.

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

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191.

Appendix. Symbols Used

i = Indexes years
n = The number of years
j = Indexes the age classes
r = The number of age classes
C_i = The actual number of fish caught in year i
C_{ij} = The actual catch of age class j fish in year i
N_{ij} = The actual number of fish from age class j in the population at the beginning of year i
F_{ij} = Instantaneous fishing mortality
M_{ij} = Instantaneous natural mortality
P_{ij} = The percentage of the fish caught in year i which belong to age class j
O_i = The estimated total number of fish caught in year i
S_{ij} = The number of fish aged in year i and found to be of age j
D_i = The deviation from average fishing mortality in year i
σ = The standard deviation for errors in total catch estimates
σ_1 = The standard deviation for deviation from average fishing mortality
σ_2 = The standard deviation for the stock–recruitment relationship