Implications of Age Determination Errors to Yield Estimates

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Abstract


Recently there has been a realization that significant errors occur in estimating ages of many fish. This development has brought about a need for mathematically based models for examining and assessing the consequences of errors in age estimates. We addressed the subject by applying known errors in age-determination to hypothetical fish species with contrasting differences in life expectancy. One species completed its life in 10 years; the other in 100 years. We also modelled salmon on the west coast of Canada as an example of a species with a life span of about one half century. We incorporated growth, and mortality rates into a stock simulation along with age-determination errors to explore the potential effects on yield estimation using dynamic pool models. Yield-per-recruit expectations increased over the true levels by as much as 19% if the only errors were from mean size-at-age. The analysis was sensitive to the behavior of the ageing error after the age of maturity. Management recommendations based on ageing methods that fail at the age of maturity can cause serious overfishing. However, the possible yield errors included over-estimates as well as underestimates depending on when the age-determination method was modelled to fail.

Résumé


On s’est rendu compte dernièrement qu’il se produisent des erreurs importantes au niveau de l’estimation de l’âge de nombreux poissons. Cette constatation a souligné la nécessité de modèles mathématiques pour estimer et évaluer les conséquences des erreurs d’estimation de l’âge. Le sujet a été traité de la façon suivante : des erreurs connues de détermination de l’âge ont été appliquées à des espèces hypothétiques de poissons dont l’espérance de vie présentait de différences marquées. Une espèce avait un cycle de vie de 10 ans, l’autre de 100 ans. Nous avons également utilisé comme modèle la morue charbonnière de l’est du Canada comme exemple d’une espèce dont l’espérance de vie est d’environ 50 ans. Nous avons introduit le taux de croissance et de mortalité dans la simulation d’un stock et les erreurs de détermination de l’âge afin d’étudier les effets possibles sur l’estimation du rendement au moyen de modèles de la dynamique en bassin. Les prévisions du rendement par recrutement étaient jusqu’à 19% plus élevées par rapport au niveau réel si les seuls erreurs se situent au niveau de la taille moyenne selon l’âge. L’analyse était sensible au comportement de l’erreur de vieillissement lorsque l’âge de la maturité était dépassé. Les recommandations de gestion qui reposent sur des méthodes de détermination de l’âge qui donnent un âge à la maturité inexact peuvent être à l’origine d’une importante surpêche. Cependant, les erreurs de rendement peuvent autant être la cause de surestimations que de sous-estimations surtout dépendant du moment où la modélisation de la détermination de l’âge prévoit que celle-ci n’est plus valable.
Introduction

Age is one of the most important variables used in fisheries science. For many fish, estimating age is difficult. However, because investigators are not aware of this difficulty, the error associated with age-determination estimates has seldom been considered in stock assessments. Beamish and McFarlane (1983) showed that in an unselected sample of 75 stock assessment papers published between 1965 and 1980 in five major journals, not one author used validated ages in the analysis. In other sciences it is fundamental to estimate error for each parameter in a calculation and to provide an estimate of how these accumulated errors affect the final result.

Some investigators believe the problem of error in age determination is unimportant because they think the error is small. This belief, of course, is paradoxical because the magnitude of the error is unknown. However a belief that errors are small appears to be the reason most investigators have ignored incorporating age-determination errors in their stock assessment models. The subject of age-determination errors in stock assessment requires an assessment of the accuracy of past and present age-determination techniques, and if important errors are present, then the consequences of these errors in determining yields and understanding biology need to be examined.

Accuracy of Age Determination

In this report we briefly review the accuracy of age-determination methods to show that errors exist. We then examine the consequences of these errors on yield from models of three populations that represent a range of life history types found in fish populations.

The accuracy of age-determination methods was re-examined by Beamish and McFarlane (1983). The standard methods that use scales or surface examinations of otoliths probably provide accurate estimates of age over the range of more rapid growth. The problem with these methods, however, is that they assume an isometric relationship between the length of the fish and the growth of the scale or otolith surface area. When growth stops or is reduced, there will be a change in the growth pattern of these structures that will result in a change in annulus development. Examples of the importance of the aging error that resulted from the use of the scale method were provided by Beamish and McFarlane (1987) for 16 species of common freshwater and saltwater fishes. In all cases, fish were found to be much older than previously thought. Examples of fish being older than previously thought are becoming more common in annulus development. The use of new age-determination methods, such as sectioning otoliths, breaking and burning otoliths, or the use of opercula and fin rays, have provided some major changes in the understanding of fish growth and production. For example, on the west coast of Canada, most of the commercially important species are now believed to be much older than previously thought (Beamish and McFarlane 1987). Nine percent of the species now are believed to have maximum ages less than 20 yr, 44% range from 21 to 49 yr and 44% range from 50 to 100 yr (Chilton and Beamish 1982: Beamish and McFarlane 1987). Even small errors are important when the maximum age of the fish is only a few years.

We believe that the example of the change in understanding of the age composition of West Coast groundfishes, the increasing account of aging error and the general lack of age validation studies, indicate the errors in the accuracy and precision of age estimates are more common than previously thought. Unquestionably, aging errors exist and the consequences of such errors need to be examined.

Methods

We developed our model with two hypothetical species of fish, one that completed its lifespan in ten years, that we called the “decadefish;” and one that completed its lifespan in 100 years, that we called the “centuryfish.” The decadefish matured at 3 years of age, and recruited to the fishery at the same age. The centuryfish matured and recruited to the fishery at 15 years. We also developed a model of a half-centuryfish from published parameters of the saffrebeak (Anaplagoma fjumbria). This species had its age of 50% maturity at 5 years, was form- uly and erroneously aged by using scales, but is at present aged with otoliths using the break and burn method (McFarlane and Beamish 1983). In our model we looked at the implications to potential yield of using each of the age-determination methods.

We arranged the models of the decadefish and centuryfish so that we first sampled the population prior to exploitation by the fishery. This meant that the estimate of the total instantaneous mortality rate from our sample was an estimate of the instantaneous natural mortality rate, $M$. The fish of this sample were put into our age-determination simulator to induce the kind of error historically been made in the similes to the decadefish and centuryfish. It is this induced error that we investigated.

To incorporate age-determination error into the model, we developed an age prior schedule of percentage errors that an age reader might make using erroneous age-determination techniques such as scale reading. The kind of errors that could occur were similar to the known age- ing errors for species that have a range of longevity (white suckers, lake trout, lake whitefish, rockfish). The percentages were set up as a matrix of coefficients giving the probability of a fish of a given age being assigned to any age including its true age (Tables 1 and 2). In addition to the published studies, our experience leads us to think that these errors are representative of errors that are being made by age readers.

For the decadefish, the simulated age reader did not recognize fish older than age 7. Fish were assigned either to the true age, or to the adjacent ages. The reader became progressively less accurate with older fish (Table 1). The chance of an age-1 or age-2 fish being called correctly
Table 1. Transfer coefficients of the decadefish as probabilities of reassignment by the age reader from the fish's true age to any age.

<table>
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<tr>
<th>Age transferred</th>
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<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
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Table 2. Transfer coefficients of the centuryfish as probabilities of reassignment by the age reader from the fish’s true age to any age. To simplify this presentation ages are given by the 16-yr interval as mean probabilities for the intervals. Year-interval probabilities were actually used in the calculations, with smoothed transitions from one 16-yr interval to the next.

<table>
<thead>
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<th>Age interval transferred</th>
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<th>31-40</th>
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<td></td>
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<td>6</td>
<td>02</td>
<td>12</td>
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<td>0</td>
</tr>
<tr>
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<td>30</td>
<td>45</td>
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</table>

was 95 and 90%, respectively. Age-4 and age-5 individuals had a chance of 80 to 30%, respectively. As can be seen from these percentages, the age-determination method largely failed after age 4.

For the centuryfish, the simulated age reader did not recognize fish older than age-40. Individuals in the first decade of life (age 1-10) had a 90% mean chance of being aged correctly. In their second decade, the chance was 82%; in the third decade, 64%; and in the fourth decade 45%. The method of age determination first failed in the third decade (ages 21-30). In fact, after age-28 there was only a 50% chance of correct age assignment. For the
most part, the errors in age determination were spread over a 3-decade age span. For example, fish whose true age was between 31–40 had a mean chance of 25% of being mis-assigned to the age range of 11–20; 30% into ages 21–30; and 45% into the range 31–40 (Table 2). Fish whose true age was 41–60 were mis-assigned to the age 11–40 range. Individuals older than 60 had a progressively increasing chance of being assigned to the 31–40 range rather than to the younger ages.

The depletion curves of number-at-age with induced error were fitted with a log-linear, least-squares regression to determine the apparent value of M. This estimated M, along with mean size-at-age with induced error, was used directly in dynamic pool (yield-per-recruit) model calculation (Guillard 1983, p. 147) of potential yield.

For the half-century fish the "reference" data that corresponded to the error-free case were the published production parameters of the sablefish determined by the break and burn method, including an estimate of the instantaneous mortality rate (M) (McFarlane et al. 1985), and von Bertalanffy parameters (McFarlane and Beamish 1983). The values, applying to fish in the Queen Charlotte Sound on the west coast of Canada, are as follows: M = 0.10, K = 0.243, W∞ = 6500 and t0 = 0.86, where K is the Brody growth coefficient, W∞ is the ultimate weight, and t0 is the age correction-factor. The numbers-at-age data "with error" were reconstructed from the older estimate of M = 0.22 from scale readings (Low et al. 1976). To derive the comparable von Bertalanffy parameters we used the same values of W∞ and t0 but adjusted K so that the fish in the age range of 5-10 years were a maximum of 0.5 kg heavier than the latter estimates. This approximated the difference between weight-at-age curves determined by break and burn methods and by scale reading (Lai 1985).

**Results**

For the decadefish the simulated induction of ageing errors shifted many individuals forward in the age distribution. There were more fish at age four than at any other single age (Fig. 1). Age 4 was the oldest age for which there was reasonable accuracy in age determination. At older ages less than half of the fish were correctly classified to the correct age. Fish accumulated at age 4 because few individuals were shifted out of this age, but many were assigned into the age from the older ages. There was a tendency to underage the fish. Because of the mis-assignments, the slope of the number-at-age line appeared to be steeper than the slope for the true curve.

For centuryfish, there were more fish in the 11–40 age range in the erroneous number-at-age curve than there were in the true distribution (Fig. 2, top panel). All fish

**FIG. 1.** Decadefish. Number-at-age for fishery-recruited ages, showing error-free data and the same sample with simulated age-determination error. The biologist would normally be aware of only the curve with induced error.

**FIG. 2.** Centuryfish. Top panel: Number-at-age plotted at 5-year intervals for the total stock, showing the sample with error-free data and simulated age-determination error. Bottom panel: number-at-age at 5-year intervals for the recruited ages. The youngest, fully recruited age (knife-edge) was 15, and the oldest, 40. Fish older than 40 were not recognized as such, and were assigned to younger ages.
over 40 were shifted to younger ages. At ages 10 and younger, the erroneous and true number-at-age curves are about the same. The greatest discrepancy between the erroneous curve and the true curve occurred in the 15–20 age group (Fig. 2, bottom panel). As with the decade-fish, the accumulation of true-aged fish and mixed-aged fish was greatest prior to the age at which the age-determination method fails. Errors occurred over most of the fishery-recruited ages. As a consequence, the slope of the depletion curve increased only a little, and appeared higher than, and almost parallel to, the true curve.

For the half-century-fish (table-fish) most individuals were younger than age 40 (98%) for the more accurate or “reference” population reconstruction. The oldest age in the sample of 3400 fish was 56. On the other hand, for the erroneous population reconstruction most of the fish were younger than age 10.97% (Fig. 5).

Our models of decade-fish and century-fish were set up so that the calculated slope of the depletion curve was an estimate of $M$. The induced errors caused $M$ to shift from its true value of 0.60 to 1.05 for the decade-fish, and from 0.050 to 0.056 for the century-fish. A biologist unaware of the age-determination error might conclude that the age-specific mortality rate of the century-fish in the last five years of life was actually very high, higher than the average rate of the younger portion of the stock, in order to account for the disappearance of the fish and the truncation of the number-at-age curve.

Weight-at-Age

When older fish were assigned to younger ages, their body weights were averaged in with those of the younger fish when the weight at age was calculated. This process caused an increase in the mean weight-at-age for the hypothetical species (Fig. 3). Most of the oldest decade-fish were assigned to age 6. Though there were only a few old fish, they were heavier than age 6-fish, and their weight increased the mean weight-at-age (Fig. 3).

Similarly, the weight-at-age curve for the century-fish was shifted upward, particularly for fish in the 10–20 age bracket. These were the ages with the greatest increases in number-at-age due to older fish being reassigned to younger ages, and so the weight increase here was not surprising. However, there was only a small increase in weight of the oldest fish, where one might expect a greater rise because of the increase in numbers at ages 39 and 40 due to reassignment. There was little increase in mean weight, however, because fish older than age 30 had grown very little.

For the half-century-fish the maximum difference in weight-at-age between the erroneous and reference data occurred at age 7. There was very little difference at age 20 (Fig. 5).

Potential Yield

The levels of error in estimates of potential yield from biased and unbiased data were examined in two stages with the dynamic pool model. (1) The addition of error solely from the biases in weight-at-age relationships, (2) the addition of error due to biases in the natural mortality rate. Natural mortality rate and age-specific weights are the two factors that play off against one another in the calculation of yield-per-recruit as a function of fishing mortality rate ($F$) in the dynamic pool model.

As expected, yield-per-recruit increased with increase in $F$, rapidly at first, and then very slowly (Fig. 4). The curves for the century-fish showed maximas, then decreasing yields, whereas the curves for the decade-fish increased asymptotically. The yield-per-recruit curves were compared by examining the differences between them at a selected level of $F$. By making the comparison at an intermediate value of $F$ ($F = 1.0$), it was easy to see that the use of biased weight data and the true value of $M$ increased the expected yield-per-recruit for both species — up to 91% for the decade-fish and 16% for the century-fish. So if there were only weight biases, yields would be overestimated.

The biased values of $M$ were higher than the true values. With an increase in $M$, more individuals would die due to natural causes, and there would be fewer fish available to the fishery. Potential yield would be less for
a given level of fishing effort. Consequently, the yield-per-recruit curves using biased M as well as biased weights were lower at F=1.0 than were the curves with biased weight alone. For the centuryfish, the lowering of the curve made the estimate of yield only 6% higher than the true estimate. In effect, the mean weight and mortality rate biases tended to cancel another. The greater bias (increase) in M in the decadefish caused a greater reduction in yield-per-recruit, so much so that the potential yield was underestimated by 63% at F=1.0.

For the centuryfish and decadefish there was little change in the age of the cohort biomass maximum with the erroneous and error-free data. For the erroneous data of the centuryfish the age was 19, and 21 for the error-free case. For the decadefish, the biomass maximum occurred at age-4 in both cases. For the half-centuryfish, the differences in the parameter values caused cohort biomass to maximize at age-8 for the error-free data, and age-4 for the erroneous data, i.e., at half the age (Fig. 6). The change in the biomass maximum in the half-centuryfish means that the optimum age at first capture, as well as F, would influence the potential yield, and so we follow the standard practice of using yield isopleths to analyze the influence of both factors acting simultaneously. For the reference data of the half-centuryfish, the yield-per-recruit maximized when fish were first taken at age-8 with an F value of 0.90 or greater (Fig. 7, top panel). However, for the erroneous data, yield-per-recruit maximized when fish were exploited as young as age-5 with an F value of 0.75 or greater (Fig. 7, bottom panel). Further, the maximum yield per recruit expected from the erroneous data was 900 g, whereas the correct value was 2500 g (Fig. 7).


Discussion

A wide range of errors in yield estimation was caused by incorrect age determination. The possible yield-per-recruit errors demonstrated here included modest over-estimates, ranging through small and large under-estimates. For a given $F$, overestimation resulted when there were biases in weight-at-age but not in mortality rate, because the biased mean weight-at-age was usually greater than the true weight values. Ageing errors caused a false increase in natural mortality rate estimates that resulted in an underestimate of yield-per-recruit. However, the true estimate of natural mortality rate would indicate a larger yield per-recruit. This does not mean that more fish can be harvested. The paradoxical situation occurs because the true lower $M$ also indicates lower production. If the tactic of setting $F = M$ (Alverson and Pereyra 1969) were adopted using the erroneously high $M$, overfishing would result. The importance of maintaining large standing stocks for older, slow growing fishes is well known for species such as rockfish.

In a recently published analysis of walleye poplolk (Lai and Gunderson 1987), it was shown that under-ageing could cause overestimation of yield-per-recruit. The overestimation was due to the bias in weight-at-age being far stronger than the bias in the mortality rate. We showed that under-ageing could lead to both overestimation and underestimated of the yield per recruit, depending on the relative strengths of bias in mortality rate and weight-at-age. The degree of bias associated with either weight-at-age or mortality rate depended on the patterns of error in assigning individual fish to specific ages. The failure of the age-determination method at a relatively young age caused a substantial upward bias in the estimation of $M$. This bias was produced by an accumulation of fish at the age range where the age-determination method failed (<50% correct age-classification). Also, when decade-fish were misassigned into a narrow portion of the true age range through under-ageing, mortality rates determined from the age distribution were strongly biased, and the yield-per-recruit error was large. In contrast, when the age-determination method broke down gradually over a large range of ages (centuryfish), the estimate of the mortality rate was only slightly biased upward, and yield-per-recruit error from this source was small.

Weight biases were substantial except when the fish being mis-aged were approaching $W_{ma}$, e.g., if individuals at sizes close to ultimate weight were reassigned to younger ages that were also close to the ultimate weight, little weight bias occurred. When biases in both weight and $M$ were in the model, errors in estimated yield-per-recruit were somewhat reduced because the effects of the biases on yield tended to cancel each other.

The half-centuryfish was modelled with sablefish data. As with the hypothetical species, age-determination error led to a large overestimate in $M$. The erroneous estimate of $M$ was 0.22, and the true estimate was 0.10. However, there were only small errors in weight-at-age because older fish in general increased very little in weight. At age-7, where weight-at-age error maximized, the erroneous weight was only 14% (0.5 kg) higher than the true weight, and the erroneous $K$ was only 13% higher than the more accurate $K$. As with the decadefish, yield-per-recruit was underestimated due to the bias in mortality rate. If the erroneous $M$ was used to decide $F$, there would be over-fishing.
The ageing error that contributes to the decrease in yield-per-recruit estimates is associated with the higher estimate of M. The effect of overestimating M was considered by Bradford and Pye (1982) by examining the relationship between mortality and yield. In addition, the erroneous yield-per-recruit diagrams suggest that the age at first capture should be age-5, though only half of the fish at this age are mature. Since the erroneously estimated value of F would be 0.70, the corresponding survival rate would be only 40% per year (S= ε−0.7M, where F = 0.70). The fishing rate would reduce the spawning stock and overfishing would be likely.

Because there is no Fopt for the decidafish, one might use the conservative tactic of setting F at a value equal to M (Alverson and Perry 1969). There are theoretical reasons that this policy would sometimes prevent: recruitment overfishing (Shepherd 1982). Due to age-determination errors this F value would be erroneously high because M was estimated as too high (errorous M estimate level = 1.05; true level = 0.60). If management control were made on the basis of fishing effort, say allowing 1.75 times as such effort as at present (by the ratio 1.05/0.60), then the result would be an overfished stock because of the high effort that was recommended.

In the case that an estimate of recruitment is made with a catch-at-age analysis technique such as virtual population analysis, use of erroneous percentage age compositions, and a much inflated M value in the equations would lead to a gross overestimation of recruitment levels. More specifically, VPA would use the erroneously high M value iteratively (Gulland 1965; 1983) to produce a multiplicative error in the estimation of starting-year-class sizes. With an erroneously high M, the method would calculate that the number of fish dying due to natural causes was greater than actually occurred. These deaths would be incorporated as part of the starting-year-class size (before natural mortality). The error would be compounded by the age-determination error incorporated in the percents age-composition figures. These percentages would determine the age composition of the catch that is used by the VPA equations. The bias in these percentages will inflate the estimation of starting cohort size. The resulting quota would be higher than the quota using a true value of recruitment. In this case an a priori estimate of the resulting error is not possible. Since the Y/R curve is erroneously low, re-scaling with an erroneously high estimate of recruitment could be higher or lower than the true potential yield.

The effect of biased M and weight-at-age depends to some extent on the particular yield model being used. We have chosen the example of the dynamic pool model because it is so widely used in fish stock assessments. In addition, the principles of yield estimation utilized in this type of model are incorporated into other age-structure models, and so the effects of the biases discussed here would be similar. Nevertheless, we would expect that other stock assessment workers might find it useful to test the most appropriate model for their situation with the kind of age-determination error presented in this paper.

We examined three life history types to study the effect that a management strategy based on erroneous age determinations would have on stocks. The decidafish represented a relatively short-lived species typical of species such as Pacific cod, walleye pollock and Pacific hake. A second life history type was represented by sablefish. This life history type has a relatively long life. In the past it was thought that only a few fishes had this type of life history, however, the use of new methods of age determination has shown that a number of commercially important fishes, such as rockfish, lake trout and lake whitefish are considerably older than previously thought. The third hypothetical life history type is a species that is aged by a method that does not break down until well after the age of maturity, producing inaccurate ages for the oldest fish in the population. We are not aware of many situations, other than spiny dogfish, where the ageing method breaks down well after the age of maturity. However, it is possible that more examples will be found as age-determination techniques are validated. Rockfish have the live expectancy of the sablefish, but the ageing error breaks down more like the decidafish. Other life history types could be examined, however, we believe we have demonstrated the importance of considering ageing error in stock assessment models.

This symposium was about errors in stock assessment models and the implications for yield estimation. We found age determination errors can cause serious biases in vital parameters and subsequent yield estimations. The errors have reduced effect when the method of age determination falls gradually over a broad range of ages in the middle of the lifespan. The errors are critical when the method fails in the age-range prior to the age at which cohort biomass is maximized and it is this case that is the most common type of age determination error.

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References


