# A Bayesian approach to assigning probabilities to fish ages determined from temporal signatures in growth increments<sup>1</sup>

Derek H. Ogle, Ronald C. Pruitt, George R. Spangler, and Michael J. Cyterski

**Abstract**: A Bayesian approach for assigning probabilities to ages assigned by the temporal signature technique is developed and applied to a sample of fish. Temporal signatures are characteristic growth patterns found on fish calcified structures that can be used to assign ages to fish that exhibit only partial growth histories. Bayes' theorem is used to calculate probabilities of age assignments. We develop a likelihood function for the technique based on normal probability theory. This likelihood function and the intuitive sum of squares method used in previous implementations of the technique are closely related. In addition, we show how a prior probability function can be constructed from independent prior information or from an analyst's interpretations of the scale margin. Finally, we interpret the posterior probabilities of age assignments for fish from a real example.

**Résumé**: Nous avons mis au point et appliqué à un échantillon de poissons une méthode bayésienne permettant de calculer la probabilité des âges obtenus au moyen de la technique des signatures temporelles. Les signatures temporelles sont des signes de croissance caractéristiques observés sur les structures calcifiées des poissons et permettant d'estimer l'âge des sujets qui ne présentent qu'une historique de croissance partielle. Le théorème de Bayes permet de calculer la probabilité de cette estimation. Nous présentons une fonction de vraisemblance que nous avons élaborée pour cette technique à partir de la loi normale; cette fonction est étroitement liée à la méthode intuitive, fondée sur la somme des carrés, qui avait été utilisée pour les applications antérieures de la technique. Nous montrons ensuite qu'une fonction de probabilité a priori peut être élaborée à partir de données préalables indépendantes ou des résultats de l'interprétation de la marge des écailles par un analyste. Nous interprétons enfin la probabilité a posteriori des âges attribués aux poissons, au moyen d'un exemple réel.

[Traduit par la Rédaction]

### Introduction

Ogle et al. (1994) introduced the temporal signature technique for assigning age to a fish that had ceased recording annual growth on its scales. The temporal signature technique is the matching of characteristic patterns found on the reliably observed increments of an individual to the growth history observed for that species at a particular spatial scale (e.g., stock, lake, region). The underlying principle of the temporal signature technique can be illustrated with the following hypothetical example. First, assume that a method for estimating the "expected growth history" of all year-classes (for all reasonable ages) has been developed for a population of fish (e.g., Ogle et al. (1994) and Cyterski and Spangler (1996a, 1996b) used linear models). Second, assume that eight reliable

Received June 22, 1995. Accepted March 4, 1996. J12970

**D.H. Ogle<sup>2</sup> and G.R.Spangler.** 200 Hodson Hall, Department of Fisheries and Wildlife, University of Minnesota, St. Paul, MN 55108, U.S.A.

**R.C. Pruitt.** 270A Vincent Hall, School of Statistics, University of Minnesota, Minneapolis, MN 55455, U.S.A.

**M.J. Cyterski.** Department of Fisheries and Wildlife, Virginia Polytechnic University, Blacksburg, VA 24061, U.S.A.

- <sup>1</sup> Journal reprint No. JR412.
- Author to whom all correspondence should be addressed. Present address: Northland College, 1411 Ellis Ave., Ashland, WI 54806, U.S.A. e-mail: dogle@wheeler.northland.edu

annuli were observed on the scales of a fish of unknown age captured in 1995 from the same population. A statistic (e.g., concordance sum of squares (CSS; Ogle et al. 1994) or Pearson correlation coefficient (Cyterski and Spangler 1996a, 1996b)) is then calculated to describe the relationship between the observed growth increments and the expected growth history of each year-class. The year-class with the lowest CSS or highest correlation is the estimated year-class for the fish. Assume for the hypothetical fish that, on the basis of the CSS, the best predicted year-class was 1971 and the next best predicted year-class was 1978. Ogle et al. (1994) and Cyterski and Spangler (1996a) would have simply accepted 1971 as the best estimated year-class and assigned an age of 24 (i.e., capture year – year-class) to this fish.

A singular assignment of age to a fish ignores the uncertainty about that assignment. In the hypothetical example, it is important to know how much more likely 1971 was than 1978 as the correct year-class for the fish. Quantitative estimates of this likelihood could and should be used in the decision-making process. For example, probabilistic statements about the uncertainty of an age assignment can be used by the analyst to assign an age when one age has a suitably high probability, to perform further age assignment analyses using the probability information, or, in some cases when many ages have low probabilities, to discard the fish from the sample. In addition, the probability statements can be incorporated into other analyses using the age data (e.g., growth or mortality estimation).

In this paper, we use Bayes' theorem to combine general prior probability and likelihood functions into posterior probabilities for ages assigned from temporal signatures observed Ogle et al. 1789

**Table1.** List and definition of all functions, matrices, variables, and subscripts used in the Bayesian temporal signature analysis.

	Definition	Changes from Ogle et al. (1994)
	Bayesian functions	
$L(X \theta_c)$	Likelihood function	
$h(\theta_c X)$	Posterior probability function	
$g(\theta_c)$	Prior probability function	
	Matrices	
X	Measurements of observed annual increments for a fish, $[a \times 1]$	Subscripts for individual fish, number of increments, and capture year are omitted
C	Covariance matrix for the observed increments, $[a \times a]$	
Y	Design matrix to choose f of the a observed increments in X, $[f \times a]$	
$X^*$	Subset of annual increment measurements, $[f \times 1]$	Subscripts for individual fish, number of increments, and capture year are omitted
A	Age and year coefficients from fit of (8) to all fish in the population growth history sample, $[(m + k) \times 1]$	•
В	Covariance matrix for the age and year coefficients estimated with (8), $[(m + k) \times (m + k)]$	
$Z_c$	Design matrix to construct the expected growth history of the cth year-class from the coefficients in $A$ , $[f \times (m + k)]$	Closely resembles $D_{cf}$
$\mu_c$	Expected growth history for the cth year-class, $[f \times 1]$	
$D_c$	Covariance matrix for $X^* - m_c$ , $[f \times f]$	Meaning different from that in Ogle et al. (1994)
	Variables or subscripts for matric	ees
$\Theta_c$	The $c$ th year-class (e.g., 1971)	
c	Index of the year-classes (e.g., $1 = d - a_{max}$ )	Meaning different from that in Ogle et al. (1994)
d	Capture year of a fish (e.g., 1995)	
а	Number of observed annual increments on a fish, $\leq m$	
$a_{\text{max}}$	Maximum possible age for a species, $\geq m$	Same as $z$ in Ogle et al. (1994)
s, t	Shape parameters for the beta function, ≥1 (suggested)	
f	Number of observed annual increments used in comparison, $\leq a$	
m	Number of age coefficients estimated during fit of (8)	
k	Number of year coefficients estimated during fit of (8)	
	Intermediatevariables	
Z	In modified prior calculations	Meaning different from that in Ogle et al. (1994)
$b(\theta_c s,t)$	Discrete-form beta pdf	
w	In likelihood function calculations	

in a fish's calcified structures. We describe Bayes' theorem in the context of the temporal signature technique, develop general methods for identifying prior probability and likelihood functions, and illustrate the new methodology with a small subsample of the Red Lakes, Minnesota, walleye (*Stizostedion vitreum*) analyzed in Ogle et al. (1994) and Cyterski and Spangler (1996*a*, 1996*b*).

# Bayes' theorem

Bayes' theorem provides a framework for obtaining the probabilities of ages or year-class membership. If  $\theta_1, \theta_2, \ldots, \theta_n$  is a set of n disjoint possible states of nature whose union has probability one (i.e., exactly one state of nature is certain to occur) and X is an observed state of nature, then Bayes' theorem can be written as

(1) 
$$h(\theta_c \mid X) = \frac{L(X \mid \theta_c) g(\theta_c)}{\sum_{k=1}^{n} L(X \mid \theta_k) g(\theta_k)}$$

(Berger 1985; Press 1989), where  $h(\theta_c | X)$  is the probability that the state of nature was  $\theta_c$  given that X was observed,

 $L(X|\theta_c)$  is the probability that X occurred if the state of nature was  $\theta_c$ , and  $g(\theta_c)$  is the probability that the state of nature was in fact  $\theta_c$  (Table 1). The  $h(\theta_c|X)$  is called the posterior probability function (p.f.), the  $L(X|\theta_c)$  is called the likelihood function, and the  $g(\theta_c)$  is called the prior p.f. Because the denominator in (1) is constant, Bayes' theorem can be written as

### (2) posterior $\propto$ likelihood $\times$ prior

(Press 1989). In the temporal signature technique, we wish to determine the probability that a fish with observed increments X is a member of year-class  $\theta_c$ . The posterior p.f. provides this probability given the prior information and observed data for a fish.

In addition to assigning probabilities to year-class membership, a Bayesian framework for the temporal signature technique can be used to coherently incorporate useful prior information into the analysis. Examples of prior information that could be used include fish size, year-class strength, stocking information, and the scale analyst's interpretation of the scale margin. In most previous analyses, these factors were either ignored or not incorporated quantitatively into the analysis.

# **Assignment of prior probabilities**

A prior p.f. can be constructed by assigning probabilities to each year-class specifically or with a statistical distribution function. Whichever method is used, probabilities greater than 0 should be assigned only to year-classes between d-a<sub>max</sub> and d-a, where d is the year the fish was captured, a is the number of observed annual increments, and a<sub>max</sub> is the presumed maximum age of the species. This assignment corresponds to the "restriction to plausible year-classes" suggested by Ogle et al. (1994) and is a form of incorporating prior beliefs into the analysis. The maximum age should be chosen conservatively (i.e., older ages) because year-classes with a prior probability of 0 will always have a posterior probability of 0, no matter what the data indicate (Cromwell's rule; Lindley 1985).

Prior probabilities may be assigned specifically when an analyst has knowledge about specific year-classes, as illustrated in the following two examples. First, if the existence of certain year-classes is known, but their strength is not, then the prior probability of the year-classes that exist between d-a<sub>max</sub> and d-a can be set to a constant probability that is proportional to the number of year-classes that exist over that period. Second, if year-class strengths are known or are estimable, then the prior probability of year-class membership may be set proportional to the independent year-class strength estimates. In both examples the prior p.f. stated above should be modified to reflect the survival of individuals of each year-class to the capture year and the prior probability for individual year-classes that are known not to exist should be set to or very near zero

Prior probabilities may also be assigned with a probability density function (pdf) that is parameterized to reflect the analyst's prior information or knowledge about the number of increments missing from the margin of the scale. In this paper, we use a modified beta pdf as a flexible method for modeling the analyst's interpretation of the number of increments missing from the scale margin. The beta pdf could be replaced by another known probability density function. If z is defined as

(3) 
$$z = \left(\frac{\theta_c - (d - a_{\text{max}})}{a_{\text{max}} - a}\right)$$

then the prior p.f.,  $g(\theta_c)$ , is proportional (i.e., constants ignored) to the beta pdf (Lindgren 1993) modified for discrete year-classes, or

(4) 
$$b(\theta_c \mid s, t) = \begin{cases} z^{s-1} (1-z)^{t-1} & \text{for } t > 1, \ s > 1\\ 1 & \text{for } z = 0, \ s = 1\\ 0 & \text{for } z = 1, \ t = 1 \end{cases}$$

where s and t are shape parameters that will be explained shortly and c is an index for year-classes (e.g.,  $\theta_1 = d - a_{\text{max}}$ ). To be a proper p.f. with a sum of one, the probability of each state of nature ( $\theta_c$  in (4)) must be divided by the sum of the probabilities of all states of nature. Thus, we take

(5) 
$$g(\theta_c) = \frac{b(\theta_c)}{a_{\max} - a + 1}$$
$$\sum_{i=1}^{\infty} b(\theta_i)$$

Therefore, to calculate  $g(\theta_c)$  for each year-class,  $\theta_c$  is first iterated in (4) from d- $a_{\text{max}}$  to d-a and then standardized with (5).

The analyst can parameterize the modified beta function (i.e., choose s and t) such that  $g(\theta_c)$  will reflect prior information, such as their interpretation of the scale margin. If no prior information is available then a "uniform" prior p.f. (s = t = 1)should be used (Fig. 1A). If no prior information is available. but the analyst believes that the probability of year-class membership declines linearly from the last to the first plausible year-class, then a triangular prior p.f. (s = 2, t = 1) should be used (Fig. 1B). If available evidence suggests that no or few increments are missing, then an exponential prior p.f. (s > 2, t = 1) should be used (Fig. 1C). The strength of the analyst's belief that few or no increments are missing can be modeled by adjusting s. Values of s that increase from three produce a narrower distribution (i.e., more confidence that few increments are missing). If the analyst believes that there may be several increments missing from the margin of the scale then one of the domed priors (s > 1, t > 1) should be used (Fig. 1D). We suggest that neither s nor t should be less than 1 because the end points of (4) will be undefined. The expected value (i.e., mean number of missing increments) and variance for (5) is approximately

(6) 
$$E(\theta_c) = (d - a_{\text{max}}) + (a_{\text{max}} - a) \left( \frac{s}{s+t} \right)$$

(7) 
$$\operatorname{Var}(\theta_c) = (a_{\max} - a)^2 \left( \frac{st}{(s+t+1)(s+t)^2} \right)$$

The analyst may solve (6) and (7) for the parameters s and t to model a specific mean and variance for  $\theta_c$  (i.e., essentially, the number of missing increments).

# **Likelihood function from normal theory**

A likelihood function for the temporal signature technique depends on the underlying probability distributions of the observed increments and the expected growth increments for each year-class. The techniques that we develop in this paper could be generalized to any underlying probability distribution. However, for this paper, we develop the technique by assuming that both the observed increments and the expected growth histories of each year-class are normally distributed. We assumed a normal distribution because (i) we believe that this is the most likely underlying distribution for the observed increments and the estimated growth histories and (ii) the expected growth histories can be simply estimated from the coefficients estimated by the general linear model (linear growth model (LGM))

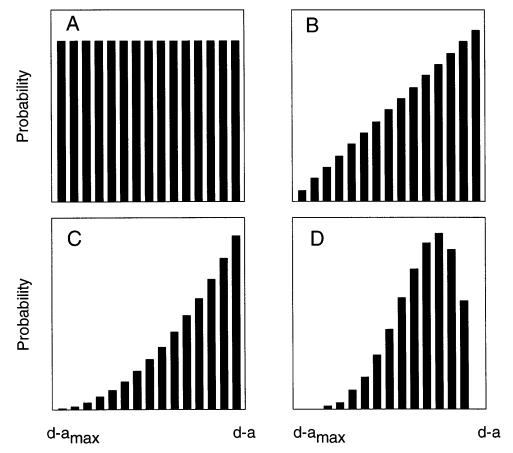
(8) expected growth increment = age effect + year effect + age  $\times$  year interaction

(Weisberg 1993). The LGM assumes that the observed growth increments and the coefficient (age and growth year) estimates are normally distributed (Weisberg 1993).

The observed increments for a fish, X, are normally distributed with a mean vector (not needed for our discussion) and covariance matrix C. The structure of C can vary according to assumptions about the relationship between the increments. Common examples of assumptions that can be modeled with

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**Fig. 1.** Four possible shapes of the discrete form of the beta (s,t) distribution: (A) uniform (s = 1, t = 1), (B) triangular (s = 2, t = 1), (C) exponential (s > 2, t = 1; s = 3, t = 1 shown), and (D) domed (s > 1, t > 1; s = 5, t = 2 shown). In these examples, a = 5 and  $a_{\text{max}} = 20$ .



C are (i) independence between increments and a constant variance (multiply identity matrix by variance), (ii) independence between increments, but a nonconstant variance (unstructured diagonal), (iii) dependence between increments and covariances subject to a first-order autoregressive function (AR(1)), and (iv) a general unstructured covariance matrix (unstructured; Jennrich and Schluchter 1986). An  $f \times a$  design matrix, Y, is used to select a subset of f increments,  $X^*$ , from the total of a observed increments. For example, to use only the first, second, and fourth increments (f=3) from a fish with six observed increments (a=6), then

$$(9) \qquad Y = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \end{pmatrix}$$

Thus, the vector of increments to use is  $X^* = YX$  and the associated covariance matrix is  $YCY^t$ .

The coefficients estimated with the LGM are put in a vector A, where the first m values are age coefficients and the next k values are year coefficients (as in Ogle et al. 1994), and the corresponding covariance matrix is B. A design matrix,  $Z_c$ , can be used to construct the expected growth history (and corresponding covariance) for the cth year-class ( $\theta_c$ ). For example, if the first, second, and fourth increments are to be compared with the first year-class (c = 1) when four age coefficients (m = 4) and six year coefficients (k = 6) were estimated with the LGM, then

$$(10) \quad Z_1 = \begin{pmatrix} 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 \end{pmatrix}$$

Similarly, if the same increments are to be compared with the third year-class (c = 3), then

(11) 
$$Z_3 = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

These design matrices are similar in theory to D in Ogle et al. (1994). However,  $Z_c$  has only f instead of m rows. Thus, the expected growth history for the cth year class ( $\theta_c$ ) is  $\mu_c = Z_c A$  and the associated covariance matrix is  $Z_c B Z_c^t$ .

The likelihood that a subset of increments,  $X^*$ , are from fish of the cth year-class can be computed from the probability distribution of the difference between the observed increments and the expected growth history of a year-class,  $\mu_c$ , which comes directly from the underlying probability distributions for each component. The difference between the observed increments and the expected growth history of the cth year-class,  $X^* - \mu_c$ , is normally distributed with mean vector 0 and covariance  $D_c = YCY^t + Z_cB Z_c^t$ . The covariance  $D_c$  thus contains a component owing to estimating the growth history ( $Z_cB Z_c^t$ ) and owing to predicting a future observation ( $YCY^t$ ). This is analogous to Weisberg's (1985) eq. 2.26 for estimating the "standard error of prediction." If we define

(12) 
$$w = (X^* - \mu_c)^t D_c^{-1} (X^* - \mu_c)$$

where  $D_c^{-1}$  represents the matrix inverse  $D_c$ , then the likelihood that the observed increments are from a fish of the cth year-class is

(13) 
$$L(X^* \mid \theta_c) = (2\pi)^{-0.5f} \mid D_c \mid^{-0.5} e^{-0.5w}$$

where  $|D_c|$  is the determinant of  $D_c$ .

The discrete likelihood function is found by computing (13) for all possible year-classes (i.e., iterating  $\theta_c$ ). Note that if no prior information is included in the analysis (i.e., a uniform prior is used) then the year-class with the maximum likelihood is the best fit for the observed fish.

# Comparison of likelihood function to CSS

The fit statistic proposed by Ogle et al. (1994), called the concordance sum of squares (CSS), can be written, with the definitions of this paper, as

(14) 
$$CSS_c = (X^* - \mu_c)^t I (X^* - \mu_c)$$

where *I* is the identity matrix. Note, for simplicity, that we have not included the subscript for number of increments included in the expected growth history because the loss of marginal increments will not be simulated in this, and most, applications of the temporal signature technique. Additionally, the technique described in Ogle et al. (1994) may be modified by weighting the CSS statistic by the inverse of the variance of each year coefficient. With the definitions of this paper (thus, including the variance of the age coefficients and the increments), this modification can be modeled by weighting the CSS statistic by the inverse of the covariance matrix,  $D_c^{-1}$ (i.e., replace I in (14) with  $D_c^{-1}$ ). Intuitively, year coefficients that are poorly estimated (i.e., large variances) will contribute relatively little to this statistic. This weighted CSS is simply w. Thus, from (13) it is easily shown that minimizing w (i.e., CSS) is the same as maximizing the likelihood function. Therefore, under these conditions, the best predicted year-class using the weighted CSS will be the same as the year-class with the largest posterior probability when a uniform prior p.f. is used.

## An example

We chose three fish from the sample of Red Lakes, Minnesota, walleye examined by Ogle et al. (1994) to illustrate aspects of the Bayesian temporal signature analysis. We did not examine the complete sample used in Ogle et al. (1994) because the posterior p.f. differs for each fish; i.e., any simple summary would result in a loss of information. However, on an individual fish basis, the results from a posterior p.f. calculated with a uniform prior p.f. should be similar to the results of Ogle et al. (1994). In the examples that follow, we compare the fish with expected growth increments for each year-class computed from the 5 age and 47 contiguous year coefficients computed by Cyterski and Spangler (1996a, 1996b). The associated covariance matrix was computed with the LGM software (Weisberg 1993). For each fish, we computed two Bayesian analyses. In the first, we used an identity matrix (with the estimated variance equal to the MSE from the fit of eq. 8) for the increment covariance matrix, a prior p.f. proportional to a modified beta (3,1) p.f., and a maximum age of 20 (Scott and

Crossman 1973). In the second analysis, we used different prior p.f. or likelihood functions to illustrate properties of the Bayesian temporal signature technique. All calculations outlined in this paper and in Ogle et al. (1994) can be made in standard spreadsheets or with special-purpose software that we have developed; this software is available on an experimental basis (i.e., not fully developed or bug free) by contacting the principal author (D.H.O.).

For fish No. 31 (captured in 1968, six observed increments, 1962 year-class), the first posterior p.f. indicated that only the 1962 and 1960 year-classes were likely, with 1962 being 2.1 times more likely than 1960 (Fig. 2). The second analysis for this fish was computed using the posterior p.f. from the first analysis as the prior p.f. and a likelihood function computed from the mean and standard deviation of the first increment observed from fish of each year-class (Table 15 from Cyterski 1995). For this likelihood function,  $\mu_c$  in (12) would be the mean first increment and  $D_c$  would simply be the associated standard deviation ( $\sigma_c$ ; 1 × 1 matrix), or (13) would look like

(15) 
$$L(X^* \mid \theta_c) = (2\pi)^{-0.5} \sigma_c^{-1} e^{-\frac{(X^* - \mu_c)^2}{2\sigma_c}}$$

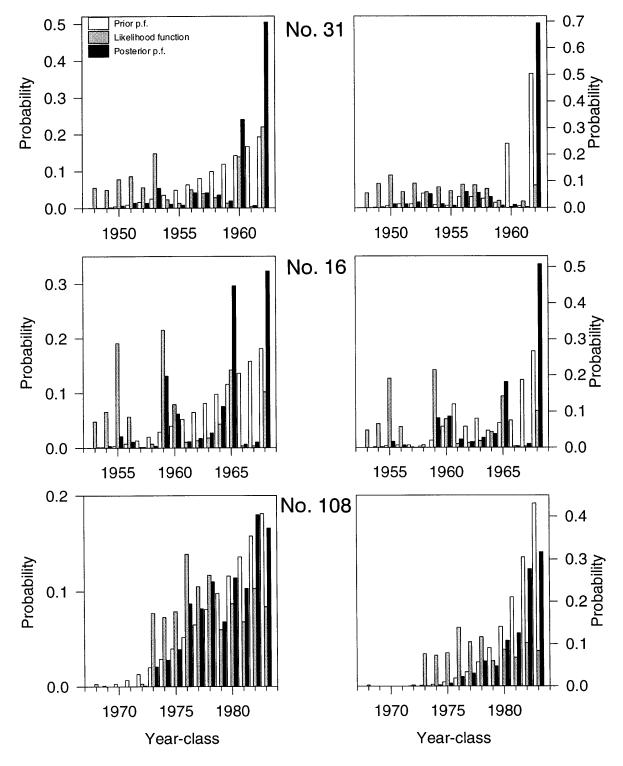
Note that the first increment was excluded in the LGM analysis because growth of age-0 walleye appeared to be unrelated to growth of older walleye in the Red Lakes (Cyterski and Spangler 1996b). With the addition of these data, the 1962 year-class was 11.6 times more likely than any other year-class (Fig. 2). These results illustrate how additional data, in this case information about the first increment, may be used to separate two year-classes with little separation in time or probability.

For fish No. 16 (captured in 1973, five observed increments, 1968 year-class), the first posterior p.f. indicated that 1968 and 1965 were approximately equally likely, with 1968 being 2.5 times more likely than 1959 and all other yearclasses having low probabilities (Fig. 2). The second analysis of this fish was computed using the same likelihood function and a modified version of a year-class strength index for this population (Table F3 from Cyterski 1995) as a prior p.f. To use this index as a prior p.f., we had to modify it to account for the survival of individuals from each year-class to the capture year. We estimated this correction by multiplying the values of the year-class strength index by the corresponding values of a modified beta (3,1) p.f. Future implementations of this correction will surely use a more sophisticated function. With this prior p.f., only two year-classes were likely, 1968 being nearly 2.8 times more likely than 1965 (Fig. 2).

For fish No. 108 (captured in 1988, five observed increments, 1983 year-class), eight year-classes had similar first posterior probabilities, with the probabilities for the 1982 and 1983 year-classes slightly higher than those for the other six year-classes (Fig. 2). This observation is consistent with the observation that the temporal signature technique is not effective when unique patterns in the year-class growth histories do not exist (Ogle et al. 1994). The second analysis of this fish was computed using the same likelihood function and a modified beta (6,1) prior p.f. With this analysis, the probabilities of the 1982 and 1983 year-classes were nearly equal and about twice as likely those of any other year-class (Fig. 2). A clear decision between year-classes in the 1980s could not be made even though the prior in the second analysis placed more

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**Fig. 2.** Two Bayesian temporal signature analyses for three Red Lakes walleye: fish No. 31 from the 1962 year-class, fish No. 16 from the 1968 year-class, and fish No. 108 from the 1983 year-class. The first analysis for each fish (left) used a likelihood function computed from the linear growth model coefficients of Cyterski and Spangler (1996a, 1996b) and a modified beta (3,1) prior p.f. The likelihood or prior probability functions were varied in the second analysis (right) to illustrate aspects of the technique: fish No. 31 used the posterior p.f. from the first analysis and a likelihood function computed from the mean (and SD) of the first increment (Cyterski 1995), fish No. 16 used the same likelihood function as in the first analysis and a modified year-class strength index (Cyterski 1995), and fish No. 108 used the same likelihood function as in the first analysis and a modified beta (6,1) prior p.f. The likelihood functions were standardized (sum = 1) so that they could be plotted on the same axis as the p.f.



weight on these year-classes. This fish is an example of a situation where the degree of uncertainty (i.e., similar posterior probabilities) should cause the analyst to explore other data (or methods) for separating year-class membership, hesitate to include this fish in further analyses, or reconsider the scale interpretation.

### **Conclusions**

The development of the temporal signature technique in this paper is an improvement over the temporal signature technique introduced in Ogle et al. (1994) for three reasons. First, and most importantly, this development provides a methodology for assigning probability and odds statements to the year-class estimates for each fish. With the original technique, only a statement relating the rank of each year-class could be reported; thus, the relative certainty of year-class membership was lost. Second, prior information and beliefs can now be coherently incorporated into the analysis. In this paper, we showed how other independent information or an analyst's interpretation of the scale edge can be used to construct a prior p.f. This information was typically lost in traditional analyses. Third, the Bayesian methodology described here is quite flexible. This framework can closely follow the intuitive method introduced in Ogle et al. (1994) or, with simple modifications, incorporate other statistical distributions for the expected growth increments or relationships between increments.

# **Acknowledgments**

We thank S. Weisberg for computational assistance. Y. Cohen, R.I.C.C. Francis, and several anonymous reviewers provided constructive reviews. This paper is published as paper No. 21 909 of the scientific series of the Minnesota Agricultural Experiment Station on the basis of research conducted under Project 77. This work is the result of research sponsored by the

Minnesota Sea Grant College Program supported by the National Oceanic and Atmospheric Administration Office of Sea Grant, Department of Commerce, under grant No. USDOC-NA90AA-D-SG149.

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