

Determining Fish Age from Temporal Signatures in Growth Increments¹

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The temporal signature technique can be used to assign age to fish that show an incomplete or indistinct growth history at the margins of their scales. The temporal signature technique matches part of an individual's "environmental" growth history to characteristic patterns found in a master chronology that was developed from reliably aged specimens of a species in a particular environment. An error sum of squares measures the concordance between an individual's environmental growth history and the master chronology. Ages assigned to walleye (*Stizostedion vitreum*) by the temporal signature technique and by examination of scales were compared to assess the performance of the new technique. Scale-age agreed with one of the three most likely signature-ages in 67–77% of the comparisons using all observed increments. These results are purposely conservative because of the methods employed and the nature of the example. All observed growth increments should be used in applying the temporal signature technique, but age may still be accurately assigned if as few as three increments are available. The temporal signature technique will perform best for species that exhibit high interannual variation in growth.

On peut recourir à la technique de la signature temporelle pour déterminer l'âge de poissons qui présentent un registre de croissance incomplet ou indistinct aux bordures des écailles. Cette technique consiste à faire correspondre une partie du registre de croissance « environnemental » de l'individu à des configurations caractéristiques retrouvées dans une chronologie maîtresse établie à partir de spécimens d'une espèce dont les âges ont été déterminés avec certitude pour un milieu donné. Une somme des carrés mesure la concordance entre le registre de croissance environnemental de l'individu et cette chronologie maîtresse. On a comparé les âges attribués au doré (*Stizostedion vitreum*) au moyen, d'une part, de la technique de la signature temporelle et, d'autre part, de l'examen des écailles afin d'évaluer la performance de la nouvelle technique. L'âge déduit des écailles concorde avec un des trois plus probables âges déduits de la signature temporelle dans 67 à 77 % des comparaisons utilisant tous les incréments observés. On fait preuve d'une prudence volontaire vis-à-vis de ces résultats en raison des méthodes employées et de la nature de l'exemple. Tous les incréments de croissance observés devraient être utilisés lorsqu'on applique la technique de la signature temporelle, mais l'âge peut encore être déterminé avec précision à partir de seulement trois. La technique de la signature temporelle donnera ses meilleurs résultats pour les espèces dont la croissance montre de fortes variations interannuelles.

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We propose a method to correctly assign age to fish from a partial growth history on scales or other calcified structures. Slow growth of older fish or resorption of previously deposited scale tissue frequently leads to underestimation of age from scales (Simkiss 1974; Beamish and McFarlane 1987; Casselman 1987). Nevertheless, the innermost regions of the scale (i.e., proximal to the focus) contain an indelible and distinguishable record of at least the first few years of an individual fish's growth. For example, a 20-yr-old fish showing eight distinct annuli before cessation of incremental scale growth contains a valid growth history of the first 8 yr of its life. In princi-

ple, this is the same record that an 8-yr-old would show had it been taken 12 yr before the 20-yr-old was taken. This paper describes a new technique, the temporal signature, that can be used to determine which calendar years were recorded on the scale, thus leading to a correct age determination by simply knowing the date of capture.

The temporal signature technique is the matching of an individual's partial "environmental" growth history to characteristic increment patterns found in an "environmental" growth history defined for that species in a particular environment. The environmental growth component is the year-to-year expression of growth regardless of age and, thus, may be called a "year effect" (Weisberg 1993). A linear model, conceptualized as

$$(1) \text{ Expected growth increment} = \text{age effect} + \text{year effect} + \text{age} \times \text{year interaction},$$

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TABLE 1. Number of fish, by scale-age and era, used to create the master chronology and assess the temporal signature technique. Only fish with a scale-age between four and eight were used to assess the temporal signature technique.

Scale-age	Create the master chronology			Assess the temporal signature technique		
	1940s	1960s	1980s	1940s	1960s	1980s
2	0	0	157			
3	0	19	569			
4	8	39	158	0	12	10
5	13	43	5	9	15	2
6	13	37	2	10	13	0
7	4	31	1	7	6	0
8	6	8	8	6	0	2
Total	44	177	900	32	46	14

can be used to estimate the separate effects and coefficients (Weisberg 1993). A master chronology is the series of year coefficients estimated from a sample of known-age or reliably aged fish from a particular environment. This is analogous to the "standardization" used by dendroclimatologists to remove nonclimatic signals (e.g., age) in a tree growth-ring series (Graybill 1982). For an individual fish of unknown age, the environmental component of the recorded portion of the fish's growth history (i.e., observed increments minus estimated age coefficients) can be compared with the master chronology to determine which calendar years were recorded on the scale. For example, the eight increments recorded on the 20-yr-old fish, corrected for age by subtracting the corresponding age coefficients (1–8) from the observed increments, can be compared with every possible starting point (year) on the master chronology. The best estimate of the individual's membership in a year-class is the initial year of the 8-yr segment on the master chronology for which the age-corrected values best match. The age of the individual is then estimated as the difference between the date of capture and the estimated year-class.

This paper demonstrates the application of the temporal signature technique for assigning age to walleye (*Stizostedion vitreum*) from Red Lakes, Minnesota. It illustrates the strengths and limitations of the technique for assigning ages to a species whose older members are difficult or impossible to age by scale inspection. The shortcomings that are discussed for this data set are no less difficult than those commonly encountered in fisheries assessments. Thus, this example provides a realistic examination of the validity of this new technique.

Methods

A master chronology for Red Lakes walleye was developed from fish collected in 89-mm (stretch measure) gill nets (Shroyer 1991; Table 1). Scales from these fish were pressed on acetate slides for viewing on a microfiche reader. An annulus, defined as the exact circulus which "cut-over" previous circuli (Shroyer 1991), was located with the aid of general criteria (Jearld 1983). Fish assigned an age older than 8 were not used in the development of the master chronology (Table 1) because scales are known to underestimate the age of older walleye (Belanger and Hogler 1982; Erickson 1983) and, on older fish, annuli near the scale margin could not be unambiguously located and measured, a requirement for applying the technique. Annual growth increments were measured with the aid of a digitizer tablet along a transect drawn from the focus to the anterior scale margin between the two centermost radii (Jearld 1983). All model fitting was performed with Weisberg's (1993) special purpose program assuming an identity, rather than a general, correlation matrix.

Model (1) was fit to the annual increment data from these samples. The estimated interaction effect was highly significant and its mean square was 1.0% of the age and 13.3% of the year mean square. A significant interaction indicates that each year-class, rather than the stock, has its own characteristic chronology. If a significant interaction occurs, then the temporal signature technique could be implemented by estimating a master chronology for each year-class rather than for the stock. However, the analysis is simpler and more intuitive if the age × year interaction explains little of the variation and the main effects can be interpreted directly. Weisberg (1993) described several techniques for diagnosing the cause of and effectively reducing a high age × year interaction. We reduced the age × year interaction by fitting a \log_e -transformed version of the conceptual model (1), namely

(2) $\log_e(\text{expected growth increment}) = \log_e(\text{age effect}) + \log_e(\text{year effect}) + \log_e(\text{age} \times \text{year interaction})$

(Weisberg 1993), and excluding the first increment. The first increment may have contributed substantially to the interaction effect because growth of young-of-the-year walleye is poorly correlated with growth of older walleye in Red Lakes (Shroyer 1991).

Coefficients for ages 2–8 and the year coefficients for three noncontiguous periods 1942–49, 1961–72, and 1980–87, referred to as the eras of the 1940s, 1960s, and 1980s, were estimated by fitting (2) to all increments (except the first) from all fish. The interaction is significant but explains little of the variation relative to the two main effects (i.e., only 6.1% of the age and 0.4% of the year mean square; Table 2) and can be ignored (Weisberg 1993). Thus, the age and year coefficients are interpreted directly and, for use in later analyses, are put into a single vector, A , with m age coefficients (=7 in this case) in the first m rows and k year coefficients (=28) in the next k rows. Each matrix and subscript used in the analysis is briefly described in Table 3.

The effectiveness of the temporal signature technique was tested with a sample independent of that used to create the master chronology (Tables 1 and 4). These fish were also collected with 89-mm gill nets but were sampled from only those fish thought to be from a year-class, c (based on scale-assigned age), represented in the master chronology. Criteria for annulus detection and measurement were the same as those used to create the master chronology. For these samples, let x_{daj} be the vector of a incremental measurements ($\leq m$) from observed annuli (first increment excluded) on scales from the j th captured fish in year d .

A simple error sum of squares was used to measure the concordance of a vector of f measurable increments ($\leq a$) with the master chronology beginning at year $c + 1$ (the addition of 1 is necessary because the first increment was ignored). This measure, called concordance sum of squares (CSS), is expressed in matrix notation (similar to equation 2.19 of Weisberg (1985)) as

$$(3) \quad \text{CSS}_{cjj} = [(y_{djj} - D_{c_j}A)^T(y_{djj} - D_{c_j}A)]$$

where A is the vector of age and year coefficients described previously, y_{djj} is a vector of m components with the first f rows

TABLE 2. Analysis of variance table for (2) fit to scale increments 2–8 from walleye used to create the master chronology.

Source	df	SS	MS	F	p
Age	6	444.017	74.003	1246.470	<0.000001
Year	27	134.085	4.966	83.647	<0.000001
Interaction	88	26.648	0.303	5.100	<0.000001
Pure error	2805	160.595	0.060		

TABLE 3. List and definition of all matrices and subscripts used in the temporal signature analysis.

<i>Matrices</i>	
<i>A</i>	age and year coefficients from fit of (2) to all fish used to create the master chronology, $[(m + k) \times 1]$
x_{daj}	measurements of observed annual increments for a fish, $[a \times 1]$
y_{dfj}	\log_e -transformed measurements of the subset of annual increments to be compared with the master chronology $[m \times 1]$
D_{cf}	design matrix to identify which age and year coefficients of <i>A</i> that y_{dfj} will be compared with, $[m \times (m + k)]$
<i>Subscripts for matrices</i>	
<i>m</i>	number of age coefficients estimated during fit of (2)
<i>k</i>	number of year coefficients in master chronology
<i>a</i>	number of observed annual increments on a fish (excluding the first), $\leq m$
<i>j</i>	unique fish identifier
<i>d</i>	capture year of a fish
<i>f</i>	number of observed annual increments to compare with master chronology, $\leq a$
<i>c</i>	a year on the master chronology
<i>z</i>	presumed maximum age of the fish

corresponding to the first *f* values of the \log_e -transformed x_{daj} and zeroes in the remaining $(m-f)$ rows, and D_{cf} is an $m \times (m + k)$ design matrix of all zeroes with the exception of *f* ones on the diagonal beginning in the upper left corner and another *f* ones on the diagonal beginning in the first row of the $(c + 1)$ st column (Table 5). Conceptually, the two diagonals of ones in D_{cf} identify the *f* age coefficients used to correct the observed growth increments for age and the *f* years on the master chronology for fitting the age-corrected increments (Table 5). For each fish, *c* was iterated for all years from 1941 to 1986 and *f* was iterated from three (increments 2–4) to *a* (all observed increments), except that comparisons with the master chronology were not made for starting years where fewer than *f* increments would be compared. The minimum number of increments compared was chosen to be three ($f = 3$) because comparisons with $f = 2$ would be limited to only two unique patterns (i.e., increasing or decreasing). Most applications of the temporal signature technique will not test individual chronologies with $f < a$. However, we iterated $f < a$ to examine the sensitivity of the method in situations where only a small number of increments may be available. With these iterations, CSS_{cfj} was determined for each fish, all possible year-classes represented in the sample, and all combinations of successive increments beginning with the second (i.e., from increments 2–4 to 2–*a*). The best predicted year-class, *c*, for fish *j* using *f* increments is the year-class associated with the lowest CSS_{cfj} . The best predicted age is the difference between the capture year (*d*) and the best predicted year-class, *c*.

The procedure just described is the analytical equivalent of “sliding” the age-corrected increment pattern of a specimen along the master chronology until a “best fit” is observed. The

TABLE 4. Total number of comparisons used to assess the temporal signature technique arranged by scale-age and the number of the last increment used in the comparison with the master chronology.

Scale-age	Number of last increment used					Total
	8	7	6	5	4	
4					22	22
5				16	26	42
6			15	17	23	55
7		6	9	10	13	38
8	3	5	5	5	8	26
Total	3	11	29	48	92	183

initial year of the best-matched interval is then taken to be the year-class of origin for that fish. This procedure closely resembles “cross-dating,” the matching of tree-ring patterns in dendrochronology studies (Pilcher 1990). Our method of measuring “best fit” (i.e., CSS) is related to the correlation coefficient often used when cross-dating tree rings (Pilcher 1990) and the “bin sorter” algorithms of some neural network applications (Caudill 1993).

The percentage agreement between scale-assigned age (scale-age) and temporal signature-assigned age (signature-age) was used as a measure of the effectiveness of the new technique to assign age. However, this measure of effectiveness is conservative because a fish’s growth history is compared with all year classes represented in the master chronology. Any real application of this technique would necessarily restrict com-

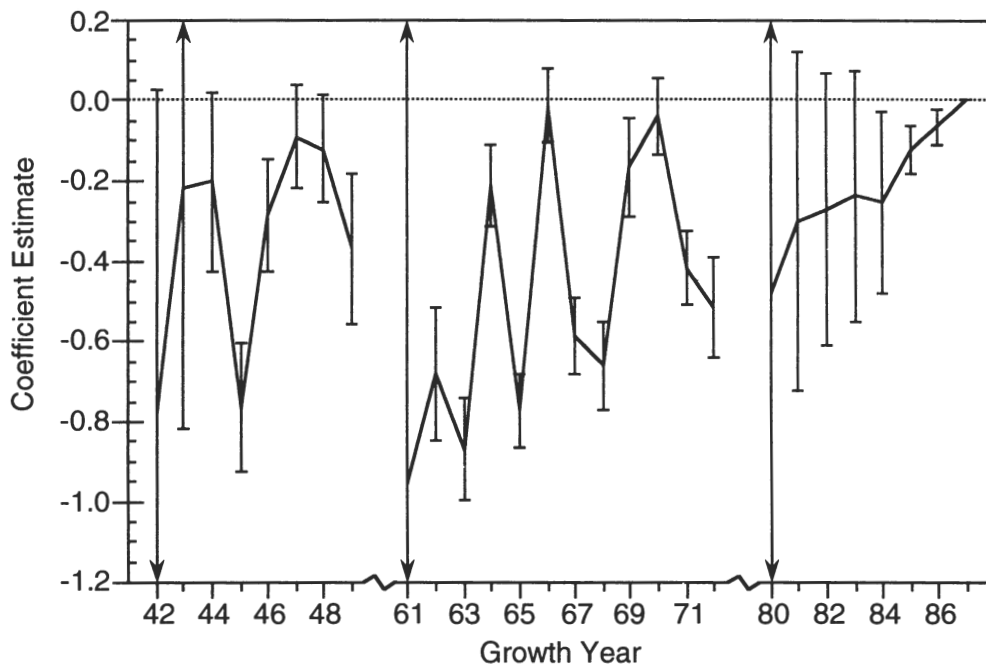


FIG. 2. Estimated year coefficients (natural log of scale increment with Bonferroni-corrected 95% confidence intervals) from (2) fit to increments 2–8 (from Shroyer's (1991) table 13). All year coefficients are relative to 1987 which was set equal to zero. This series of coefficients is considered the master chronology for Red Lakes walleye for the years represented.

inner portion of its scales. Signature-age agreed with scale-age most often when all observed increments were used. Agreement was also good when some of the observed increments were not used. This latter result reveals two important features of the temporal signature technique. First, the temporal signature technique can be used to assign age to scales with marginally indistinct or incompletely recorded growth histories. Second, the portion of the growth history that is most easily interpreted on scales (i.e., a small number of the innermost increments) can be used to assign age.

In most situations, there will be a minimum number of unambiguously observed growth increments on the inner portion of a scale that are required to accurately determine the correct age. In this example, there was little difference when only three rather than more increments were compared with the master chronology. However, disagreement between scale-age and signature-age increased when some observed increments were not used, although scale-age equaled the signature-age with the second or third lowest CSS in many of these misclassifications. Thus, all increments that can be unambiguously observed should be used, but more importantly, the temporal signature technique may be sufficient when the number of unambiguously observed increments is small, possibly as few as three.

The temporal signature technique will more accurately assign ages if the growth histories of adjacent year-classes are markedly different from each other. In long master chronologies, the growth history of a given year-class will likely closely resemble some other year-class or year-classes. However, if the year-classes with similar patterns are several years apart, then other information (e.g., capture year or size at capture) may be used to distinguish between the two. The distinctiveness of a given year-class relative to adjacent year-classes can be determined by comparing the predicted growth history of a year-class with the predicted growth history of all other year-classes and then determining the rank of the fit to adjacent year-classes. In Red

TABLE 6. Percentage of comparisons where the scale-age equaled the signature-age with the lowest (rank = 1) or one of the three lowest (rank ≤ 3) concordance sum of squares (CSS). All observed scale increments were used in comparisons where the last increment used equaled the scale-assigned age.

Scale-age	Last increment ($f + 1$) compared with the master chronology									
	Scale-age rank = 1					Scale-age rank ≤ 3				
	8	7	6	5	4	8	7	6	5	4
4					59					77
5				44	27				69	54
6			40	47	35			73	76	61
7		67	33	20	8		67	44	60	39
8	0	0	20	20	0	67	40	60	60	50

Lakes walleye, year-classes in the 1940s and 1960s were relatively distinct (median rank of adjacent year-classes 1 and 2 yr removed was 13 and 9) whereas year-classes in the 1980s were not distinct (median rank of adjacent year-classes 1 and 2 yr removed was 1.5 and 2). Distinct patterns in a master chronology will result in better age assignments because comparisons will rely more on relative pattern matching than on the absolute magnitude of the increments. Thus, the ability of this technique to determine the correct age of a fish will be influenced by the variability of external factors (e.g., climate and intra- or interspecific densities) and the sensitivity of a species' response to those factors.

Restricting the comparisons to only plausible year-classes on the master chronology would increase the accuracy of this technique. Plausible year-classes can be defined as the set of all year classes between f and z (maximum age of the species) years prior to the capture year. The restriction to plausible

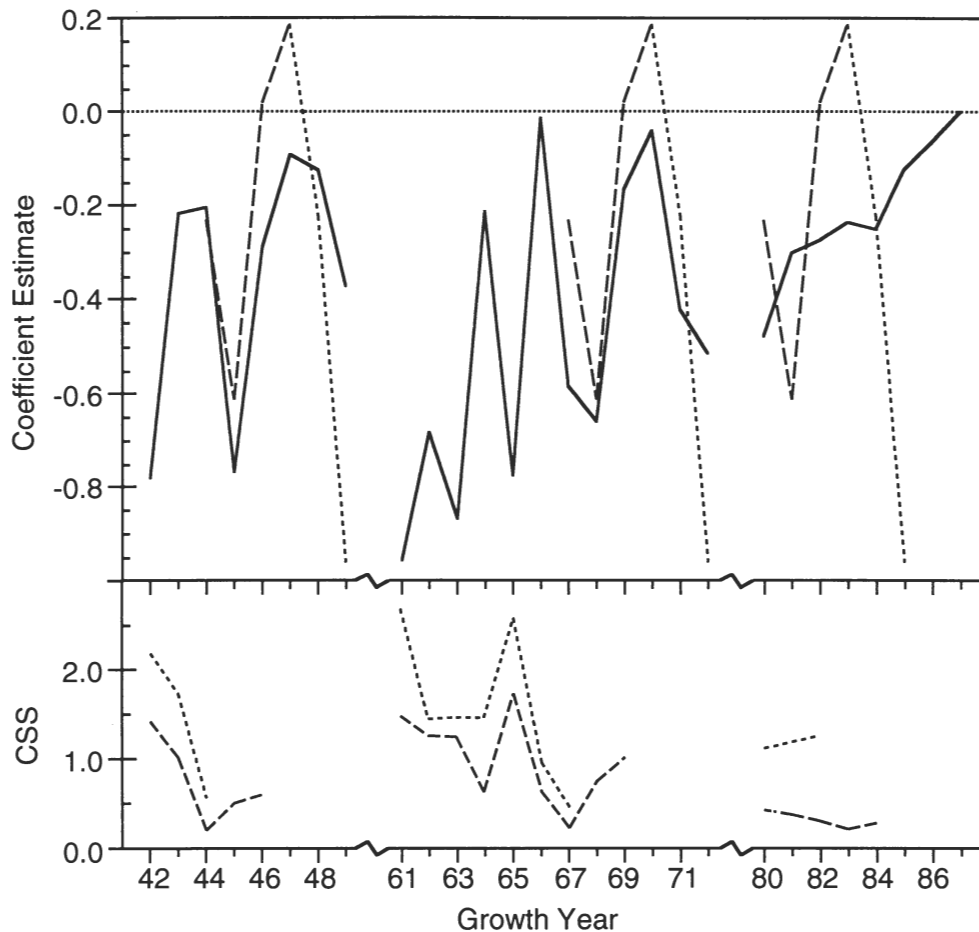


FIG. 3. Comparison of increments 2-5 ($f = 4$; dashed line) and increments 2-7 ($f = 6$; dashed and dotted line) of a Red Lakes walleye captured in 1951 and assigned an age of 8 (1943 year-class) with the master chronology (solid line) at three possible initial years (upper panel). The concordance sum of squared deviations (CSS) for all comparisons is shown in the lower panel. The growth year with the lowest CSS was 1967 (1966 year-class) for $f = 4$ and 1944 (1943 year-class) for $f = 6$.

TABLE 7. Percentage of all comparisons for which scale-age differed from signature-age by -1, 0, and 1 yr when year-classes more than 5 yr removed from the year-class determined by the scale-age were exempted from the analysis. Corresponding cells in each subtable do not sum to 100% because larger differences are not shown.

Scale-age	Last increment ($f + 1$) compared with the master chronology														
	Scale - signature = -1					Scale = signature					Scale - signature = 1				
	8	7	6	5	4	8	7	6	5	4	8	7	6	5	4
4					0						68				5
5				0	0						69	42		0	12
6			0	0	9			60	59	43			7	6	4
7		17	11	20	23		67	67	60	46		0	11	10	8
8	0	0	20	20	13	33	20	20	20	38	0	0	0	0	0

year-classes was not implemented in this analysis because the partial growth history of some samples would have been compared with only a small number of year-classes due to discontinuities in the master chronology. However, the more conservative restriction implemented in this example (i.e., restricting comparisons to years on the master chronology within 5 yr of $d-a$) resulted in an increase in the percent agreement between the two age assignment methods.

The temporal signature technique will be enhanced by the development of other measures of fit to the master chronology. The new measures may be equally simple, such as measuring the correlation between an individual's growth history and the master chronology, or more complex, an application of neural network algorithms (Caudill 1993) or development of a Bayesian approach. In a Bayesian approach, a likelihood function constructed from the concordance of a sample with

the master chronology could be used to modify a prior distribution of possible ages that was formed from a scale reader's interpretation of all features on the scale and information about the sample (e.g., length, sex, and location). Probabilities of age obtained from the updated distribution (i.e., posterior distribution) would provide an estimate of confidence in the age determined with this method. The probabilities of age in the posterior distribution could be used to assign an age to the fish (i.e., the age with the highest posterior probability) or eliminate the fish from further consideration (i.e., all posterior probabilities are equally low).

The master chronology would best be determined from known-age fish, but "reliably ageable" fish can provide a sound basis for a master chronology. Inclusion of fish in the master chronology could simply be limited to those fish that are younger than the age where age assignment becomes uncertain. The age where uncertainty begins for a particular species may be identified by analysts familiar with age determination from scales, by experience with other calcified structures (e.g., Erickson 1983), or from scale validation results.

In our example, two 1988 fish aged from scales as 8-yr-olds were assigned to the 1979 year-class by temporal signatures. This was true for all of the increment sets used to estimate temporal signature-age ($f = 3, 4, 5, 6,$ and 7) for these fish. An operculum from one of these fish yielded an age assignment of 9, which implies that the scale-age determination was erroneous. The possibility remains that our master chronology included some older fish that were misaged from scales. In spite of whatever errors of this kind are currently included within our master chronology, the scale-ages from the test sample are substantially in agreement with the signature-ages. It might be reasonable to conclude from the discontinuity evident in Table 6 for age-8 fish that age 7 is the oldest scale-age determination that should be allowed to contribute to the master chronology.

The Red Lakes walleye example represents, in our opinion, the coarsest level of resolution that might be expected from the temporal signature approach to age estimation. Discontinuities in the master chronology, simplistic analytical techniques (e.g., CSS), and purposely conservative analytical decisions (e.g., allowing an individual's growth history to be fitted to year-classes subsequent to the capture year) led to results that underestimate the ability of this technique to assign accurate ages to fish from partial growth histories. Continuous master chronologies, development of new techniques for judging the fit of a growth history to the master chronology, restrictions of plausible year-classes, and, possibly, the use of within-year patterns, especially during the first year of life, will greatly enhance the accuracy and applicability of this technique.

We believe that the temporal signature approach is superior to age determination based solely upon visual examination of scale growth. No analyst, no matter how experienced, can judge the age of a fish exhibiting only a portion of its growth history on its bony structures. Our approach removes that subjectivity and provides a method which could be automated. In addition, one of the most appealing features of this method is the assignment of probabilities to membership in specific age-classes.

The temporal signature technique will increase our understanding of fish populations in two ways. First, samples that were previously ignored because of age assignment difficulties (Carlander 1987) can now be exploited to more accurately represent and understand past fish populations. Historical collections of fish scales should, therefore, be protected because there is now a method to utilize these samples. Second, master chronologies that extend to the present can be used to assign age to scale samples from contemporary collections. Because scales are inexpensive and nondestructive structures to collect (Jearld 1983), we believe that this analytical technology will enhance the accuracy and precision of future stock assessment.

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