ESTIMATING AGE OF SEA OTTERS WITH CEMENTUM LAYERS IN THE FIRST PREMOLAR

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Abstract: We assessed sources of variation in the use of tooth cementum layers to determine age by comparing counts in premolar tooth sections to known ages of 20 sea otters (*Enhydra lutris*). Three readers examined each sample 3 times, and the 3 readings of each sample were averaged by reader to provide the mean estimated age. The mean (SE) of the known age sample was 5.2 years (1.0) and the 3 mean estimated ages were 7.0 (1.0), 5.9 (1.1) and, 4.4 (0.8). The proportions of estimates accurate to within ±1 year were 0.25, 0.55, and 0.65 and to within ±2 years 0.65, 0.80, and 0.70, by reader. The proportions of samples estimated with >3 years error were 0.20, 0.10, and 0.05. Errors as large as 7, 6, and 5 years were made among readers. In few instances did all readers uniformly provide either accurate (error <1 yr) or inaccurate (error >1 yr) counts. In most cases (0.85), 1 or 2 of the readers provided accurate counts. Coefficients of determination (R^2) between known ages and mean estimated ages were 0.81, 0.87, and 0.87, by reader. The results of this study suggest that cementum layers within sea otter premolar teeth likely are deposited annually and can be used for age estimation. However, criteria used in interpreting layers apparently varied by reader, occasionally resulting in large errors, which were not consistent among readers. While large errors were evident for some individual otters, there were no differences between the known and estimated age-class distributions generated by each reader. Until accuracy can be improved, application of this ageing technique should be limited to sample sizes of at least 6–7 individuals within age classes of ≥1 year.

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The ability to accurately estimate age has broad application in research and management of long-lived mammals. Accurate determination of individual age is fundamental to estimating accurately age structure in populations as well as age-specific measures of reproduction, growth, or survival. The use of cementum deposits in the teeth of mammals as an indication of age has become routine (Grue and Jensen 1979, Fancy 1980, Perrin and Myrick 1980). Apparent layering of cementum is a consequence of intra-annual (seasonal) variation in growth (Klevesal' 1980) resulting in a density gradient in annual deposition. Variation in the distinction of cementum deposits occurs among and within species, and may result from inter-annual variation in growth caused by environmental (e.g., temperature or daylight) or physiological (reproduction, estivation or nutrition) factors. Therefore, accuracy in assigning ages to individuals based on cementum deposits can vary both among and within species. For example, based on individuals of known age among some carnivores, accuracy estimates (proportion of estimates without error) range from 0.88 in black bears (*Ursus americanus*; McLaughlin et al. 1990), 0.84 in grey seals (*Halichoerus grypus*; Mansfield 1991), 0.60 in grey wolves (*Canis lupus*; Goodwin and Ballard 1985), to 0.32–0.45 for polar bears (*Ursus arctos*; Hensel and Sorensen 1980).

Over the past 20 years, layers in sea otter teeth have been used to develop age-specific population data, as well as individual life history data. However, little verification that these layers represent annuli has occurred. Assumed stability in annual environmental and nutritional factors were responsible for the lack of annual growth layers found in sea otter teeth (Kenyon 1969). However, following development of staining procedures, Schneider (1973), concluded that all sea otter teeth display cementum layering, although some are more regular and distinct than others. Furthermore, he found 7 annuli in a single captive sea otter known to be 7 years of age, implying the deposits may represent annuli. Assuming cementum deposits represented annuli in sea otter premolars, Garshelis (1984) developed a method for estimating age, using morphological features such as head color, length, weight, and tooth wear. Comparing cementum counts to estimated or known ages of 10 sea otters from California, Pietz et al. (1988) concluded that the accuracy of the technique as an indicator of age for sea otters was similar to other species. A neonatal line in the dentine and enamel was identified from Russian sea otters, and estimated ages of juveniles were obtained by counting daily layers subsequent to the neonatal line (Ryzanov and Klevezal' 1991). They also suggested the first cementum layer's position, relative to the root tip, could be used to determine if deposition occurred during the first or second winter of life. Based on the assumption that age estimates from tooth sections are accurate, several authors have recently provided age-specific survival and reproductive data for sea otters based on the use of cementum layers to estimate age (Garshelis et al. 1984, Siniff and Ralls 1991, Bodkin et al. 1993, Jameson and Johnson 1993).

Despite the increasing use of cementum deposits as annuli and the need to validate any age estimating technique with known age samples (Dapson 1980), the accuracy of cementum layers for estimating age has not been tested for sea otters beyond that described above. During the past 2 decades, large numbers of sea otters in California and Alaska have been captured, marked, and released. Over time, many members of this sample were either recaptured or their carcasses recovered. From these recovered animals, a first premolar was extracted and archived, providing a tooth from an animal of known age. In this paper we examine for the first time the accuracy and precision of using cementum layers to estimate sea otter age by comparing known ages to estimated ages based on premolar tooth samples. We describe accuracy by comparing the mean estimated ages of each of 3 readers to the known ages. We evaluate precision by comparing mean estimated ages between replicated tooth samples within reader. Finally, we compare the age distributions generated by each reader to the known age distribution and provide recommendations for application of the ageing method and future research to improve accuracy.

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METHODS

In California and Alaska, dependent (<6 months of age) and juvenile sea otters estimated to be <1 year old, based on weight, were marked with uniquely numbered/colored plastic tags (Temple Original Cattle Ear Tag, Temple, Tex.) on their rear flippers. One or more vestigial first premolar teeth were removed from recaptured otters or from beach-cast carcasses of those otters marked at ≤1 year of age. Teeth were air-dried following tissue removal and stored in paper or glass containers. Each tooth was decalcified in 1N hydrochloric acid, and sectioned longitudinally at 14 μm with a rotary microtome (Am. Optical Model 820). Four sections were taken at or near the midline from each tooth. Sections from 1 or 2 teeth (8 sections) were mounted on a single glass slide, stained with Giemsa solution (Ricca 3250-16; Stone et al. 1975), and coverslipped. Counts of cementum deposits were made through a variable power (20–160X) dissecting microscope under transmitted light or with a Leitz compound microscope at 60–250X. We calculated the expected number of cementum deposits (known age) by estimating a birthdate (based on weight and dependency status of sea otter at capture) and an annual cementum deposition date of 1 March (Ryzanov and Klevezal' 1991).

We examined premolars from 20 known age sea otters, aged 0–14 years. Twelve (0.60) were dependent at the time of first capture (<0.5 yr; Jameson and Johnson 1993). The mean weight and standard error (SE) of dependent otters was 6.8 kg (SE = 0.93). The mean weight and SE of the remaining 8 independent otters was 13.0 kg, (SE = 0.95) indicating an age of <1 year. The sample consisted of 11 females and 9 males, 5 of which were from Alaska and 15 from California.

Three readers experienced in reading sea otter tooth sections independently counted the number of cementum deposits in our sample. Each tooth sample provided 4–8 sections that were examined, from which one estimate of the age was made. In addition, 14 of the 20 teeth were represented by a second premolar tooth from the same animal, that provided 4–8 replicate tooth sections, so that our study consisted of 20 independent premolars and a sample of 14 replicate premolars. The sample was read 3 times by each reader. All readings were conducted independently, without knowledge of the known age of the sample, results of other readers, or their own previous results. Following each reading, the complete sample was renumbered randomly to reduce potential recognition bias. Data collected for each tooth during each reading included the estimated age (based on the no. of cementum layers), a certainty code, and a histology code. The certainty code reflected the reader's level of certainty in the estimate, based on the distinctiveness and continuity of the layers within and among tooth sections and the estimated age of the animal: A (high confidence in reading); B (moderate); C (low). The histology code reflected the condition of the tooth sections: A (normal), B (broken), or C (abnormal).

Accuracy was calculated as the proportion of mean estimated ages with ≤1 year differences from the known age, for each reader (n = 20). Precision was estimated within reader by comparing mean counts of tooth sections from a different premolar from the same animal (n = 14).

The distributions of mean estimated ages and of known ages for the sample of 20 teeth did not meet the assumption of normality. Therefore, comparisons among and within reader, as well as comparisons with known ages were analyzed with a Friedman randomized block analysis of variance on ranks with tooth sample as the block (1-way repeated measure ANOVA). Multiple comparison procedures (Dunnett's method comparing estimated age against known age; or Student-Newman-Keuls method comparing between readers) were used to isolate the group or groups that differed from the rest. The Friedman randomized block ANOVA (or the Mann-Whitney rank-sum test when only 2 classes were present) was used to test for differences in errors (the difference between estimated and known age) within reader, by histology code, reliability index, and sex of the otter. Linear regression and the standard error of the estimate of y for a fixed x (S_{yx}) was used to quantify the association between estimated and known age within reader. The t statistic was used to test for differences in regression coefficients between readers and expected intercepts of zero and slopes of 1. The estimated and known age class distributions of the samples were compared with Chi-square analysis.

Paired t-tests were used to compare estimated ages of the 14 replicate tooth samples, within reader. Friedman randomized block ANOVA on ranks was used to compare the 2 median estimated ages from the 14 replicate tooth sample readings to the median known age. All data were tested for normality and equality of variance before analysis. Significance for all tests was assigned a priori at ≤0.05. All statistical analyses and tests of significance used SigmaStat statistical software (Jandel Scientific, San Rafael, Calif.).

RESULTS

The actual mean age of our otters was 5.1 years, while the mean ages (SE) estimated by the 3 readers were 7.0 (1.0), 5.9 (1.2), and 4.4 (0.8) for readers 1, 2, and 3. Median age estimates among readers differed significantly (χ^2 = 28.3, 2 df, P < 0.0001), with no two readers being similar (Student-Newman-Keuls multiple comparison procedure, P < 0.05). In addition, the median estimated ages differed significantly from known age among readers (χ^2 = 30.6, 3 df, P < 0.0001), with reader 1 differing from the known age (Dunnett's method, q' = 4.94, 1 df, P < 0.05) but not readers 2 or 3 (q' = 1.74 and 1.90). Because of this difference among readers, we made

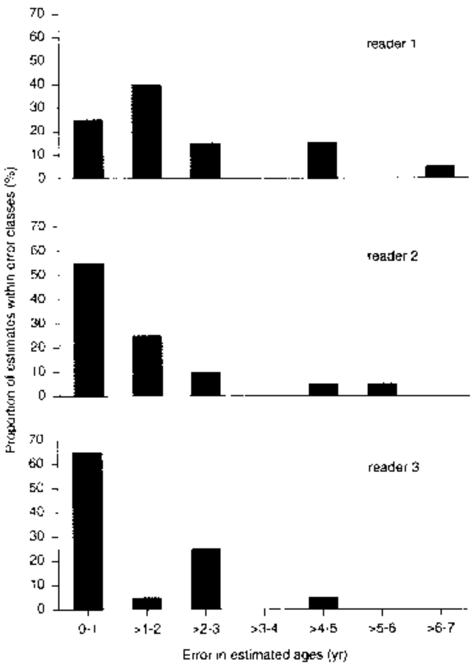

Fig. 1. Accuracy of estimated ages, by reader, for a sample of 20 sea otters whose ages are known to ≤1 year.

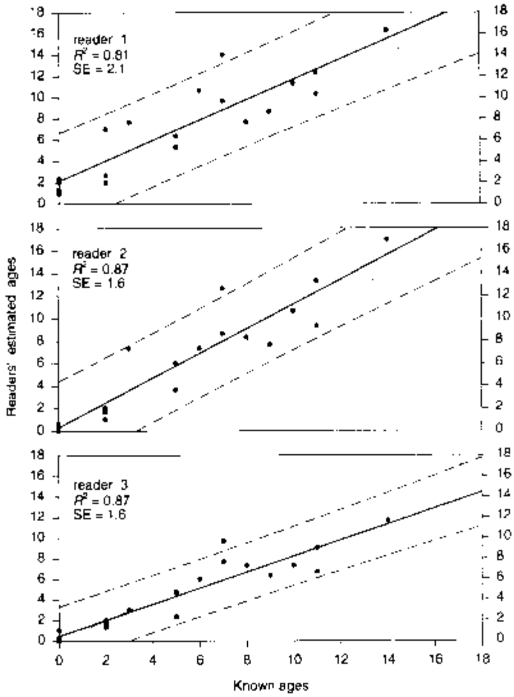

Fig. 2. Plots of mean estimated ages against known ages. Ninety-five percent prediction interval, coefficient of determination, and standard error of the estimate, by reader (. . . . . . . expected line, assumes no error). Intercept of reader 1 significantly different than 0. Slope of reader 3 significantly different than 1.

all subsequent comparisons by individual reader with known ages.

Mean errors greater than 3 years were uncommon: 0.20, 0.10, and 0.05 of the estimates for readers 1, 2, and 3 (Fig. 1). Proportions of estimates with errors ≤2 years were 0.65, 0.80, and 0.70 . The proportions of mean estimates with errors ≤1 year (our definition of accurate) were 0.25, 0.55, and 0.65 for the 3 readers. There was no significant relation between either the certainty or histology code and the mean error, for any reader ($P \geq 0.13$, 0.60, and 0.31, for readers 1, 2, and 3). There was also no significant relation between the mean error of any reader and the sex of the sea otter being aged ($P = 0.76$, 0.52, and 0.54 for readers 1, 2, and 3).

The relation between estimated age and known age differed slightly among readers, suggesting individual biases in counting cementum layers (Fig. 2). The estimates of reader 1 were consistently greater than the known age, and the y intercept of the regression line was significantly different than zero ($t = 2.95$, 19 df, $P < 0.01$). Reader 2 closely approximated known age in the younger ages, tending to slightly overestimate as age increased. Reader 3 closely approximated known ages in the younger age classes but consistently underestimated age, as age increased. The slope of the regression line of reader 3 significantly differed from 1 ($t = -3.25$, 19 df, $P < 0.01$). Coefficients of determination (R^2) for known age (independent variable) regressed against mean estimated age (dependent variable) ranged from 0.81 to 0.87 (Fig. 2).

Maximum (mean) errors in age estimates were: reader 1 = +7.0 years (+1.9), reader 2 = +5.7 years (+0.8), and reader 3 = −4.3 years (−0.7). In 17 of 20 samples, the mean estimate of age differed from the known age by ≤1.0 year, for at least one reader (Fig. 3). Reader 1 provided the best mean reading 7 times; reader 2, 8 times; and reader 3, 12 times. For 7 samples, 2 readers shared estimates that were equally close to the known age. In 3 of the 20 samples no reader obtained an accurate estimate (error ≥1 yr) and for those 3 estimates mean errors ranged from 1.3 to 5.7 years. When known ages were regressed against the estimated age with the lowest error among readers, the coefficient of determination was high ($R^2 = 0.97$, SE = 0.73).

Although we found differences in each reader's ability to estimate age accurately, those dif-

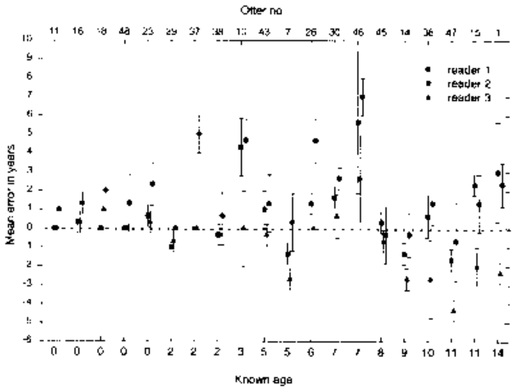

Fig. 3. Comparison of differences between estimated and known ages of 20 sea otter premolar tooth samples, by reader. Bars represent ±1 SE from the mean.

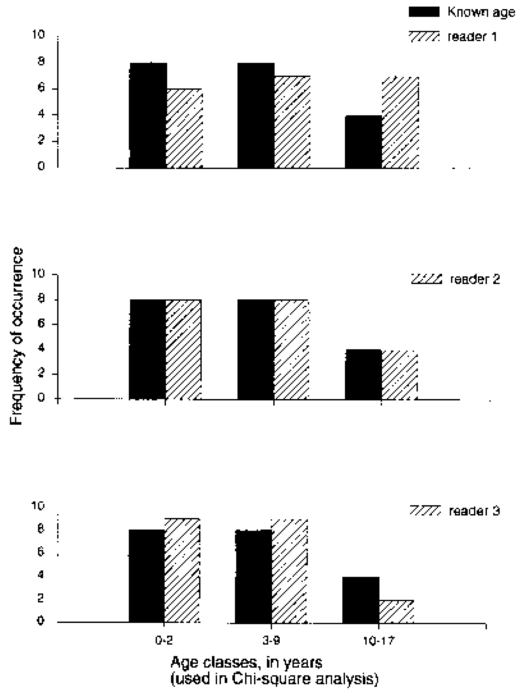

Fig. 4. Distribution of known and estimated sea otter age classes by reader.

ferences did not bias the distribution of estimated versus known age classes. We partitioned the data into 3 (0–2, 3–9, 10–17 yr) age classes that are commonly used in age-specific analyses (Fig 4). Chi-square values were 1.17 (2 df, $P = 0.56$), 0.00 (2 df, $P = 1.00$), and 0.78 (2 df, $P = 0.68$) for readers 1, 2, and 3. The median number of observations per cell was 7 (range 2–9).

To meet the second objective of this study, we examined consistency of estimates within reader by comparing mean estimated ages between 14 paired tooth samples examined independently. The actual mean age of these 14 replicate samples was 9.1 years (SE = 0.82), compared to 5.1 years (SE = 0.99) for the sample of 20. Mean estimated ages ranged from 6.7 to 10.1 years (Table 1). No statistical differences were detected between the mean estimated age of the first and second replicate readings within observer (Table 1; reader 1, paired $t = -0.45$, 13 df, $P = 0.66$; reader 2, $t = 0.11$, 13 df, $P = 0.68$; reader 3, $t = 0.38$, 13 df, $P = 0.71$). In 11 of the 14 repli-

Table 1. Mean estimated ages for replicate tooth samples, by reader and assignment of "best" reading (lowest error) to reader: "a" indicates reader(s) achieving most accurate reading of first replicate and "b" indicates reader(s) achieving most accurate reading of second replicate (column means and SE at bottom of table).

Known age	Mean estimated ages by reader						"Best reader"		
	1a	1b	2a	2b	3a	3b	1	2	3
3	7.7	6	7.3	5.3	3	2			a,b
5	5.7	5.3	3.7	4.7	2.3	1.7	a,b	b	
6	9.7	11.3	8.3	7.3	6.7	6			a,b
7	8	8	7.7	7	3	3		a,b	
8	9.7	9	8.7	8.7	7.7	7.7			a,b
9	8.3	9	7.7	9.3	6.3	6	a,b		
10	10.3	11.3	11.3	11	10	10			a,b
10	10	10.3	10.7	11.7	8.3	9	a,b		
10	11.3	9.3	10.7	12.7	7.3	3.7	b	a	
11	10	13.7	11	12.3	6.7	7.3		a,b	
12	11	10.7	16.3	15.3	5.3	8.7	a,b		
12	10.7	12.3	11.7	13.7	5.3	5.7	b	a	
12	10.3	10.7	9.3	8.7	6.7	6.7	a,b		
14	15.3	13.7	15	11	11	10	b	a	
9.1	10.1	10	10.1	9.6	6.7	6.2	Mean		
0.8	0.6	0.6	0.9	0.8	0.7	0.7	SE		

cated teeth the best (lowest error) mean estimated age was provided by the same reader for both readings (Table 1). In one of the 14 replicate samples, the best reading of one of the other readers equaled one of the best reader's 2 estimates.

While we found the median age estimates of readers 2 and 3 accurately reflected the true age of the sample of 20 otters in the first component of this study, this pattern did not hold in our replicate dataset of 14. Median age estimates provided by readers 1 and 2 did not differ from actual age (reader 1, χ^2 = 2.0, 2 df, P = 0.37; reader 2, χ^2 = 4.68, 2 df, P = 0.09), but did for reader 3 (χ^2 = 11.4, 2 df, P = 0.003, Friedman randomized block ANOVA on ranks).

DISCUSSION

Our data suggest that the differences in estimates among readers was a result of differing criteria used by each reader. Accurate readings (error $\leq$1 yr) were provided by all readers for relatively few samples (0.20; Fig. 3). In most instances (0.65) 1 or 2 readers provided accurate ages, and rarely did no reader (0.15) provide an accurate estimate. Reader 1 apparently considered some lines of deposition as distinct annuli that readers 2 and 3 considered as components of a single annuli or "complex annuli." Reader 3 tended to underestimate ages, likely by considering 2 depositional layers as a single annuli. Two periods in the sea otter's life occasionally appeared to result in indistinct cementum deposition. The first in the developmental period, ages 0–3, the second in aged animals, >10 years old. While the criteria used by any single reader may not apply equally to all animals in our sample, those criteria used by all readers, when appropriately applied will provide estimates close (<1.0 yr) to known ages in most (0.85) instances. Analyses comparing the most accurate (lowest error) of the 3 readers' estimates to known ages suggests an upper limit to accuracy may be about 0.85 (R^2 = 0.97).

The agreement between replicate readings in our study (Table 1) suggest that criteria used in counting deposits were applied consistently within reader. This was demonstrated by the same reader providing the most accurate readings in 11 of the 14 replicate tooth samples. This consistent application of criteria also was evidenced by comparing the results of the 2 components of this study. In the accuracy component where the mean known age = 5.1 years, reader 1 significantly overestimated the known ages, while reader 3's mean estimate did not differ from the known age. In the precision component where the mean known age = 9.1 years, counts made by reader 3 were significantly lower than the known ages, while reader 1's mean age was not different from the known age. These comparisons demonstrate biases of these readers (Fig. 2) and their consistent application in estimating age. A similar pattern of consistency within reader was demonstrated by Pietz et al. (1988), independent of accuracy.

The extent to which the actual age of individuals in our sample is known varies because of a number of sea otter life history characteristics. Most of our sample (0.60) consisted of dependent pups at initial marking so potential error in our age at recapture or recovery should be <3 months. The weights of independent otters at initial marking ranged from 8.2 to 17.3 kg, and include the average weight at weaning for California sea otters ($\leq$13.6 kg; Riedman et al. 1994). Therefore, we recognize a potential source of error of up to 1 year in 0.40 of our "known" ages of otters independent at initial capture because of individual, inter-annual, and spatial variation in dependency periods and estimated weaning weights. In addition, we were able to count only cementum deposits in discrete whole numbers, while we recognize that age is a continuous variable, as sea otters are born throughout the year (Kenyon 1969). Because of these potential sources of error in assigning initial "known" ages, we consider counts of cementum deposits that differ by less than 1 year to be accurate. Our estimate of accuracy (0.25–0.65) in this ageing technique is similar to estimates of accuracy from other carnivores (0.32–0.88). A 1:1 relation (without error) between the estimated number of cementum deposits and known age has not been described for any long-lived species.

The accuracy of age estimates based on cementum layers depends on how strongly cementum deposition is influenced seasonally. The process of cementum deposition may be related to one or more factors, including environmental conditions, resource availability, physiology, or behavior (Law 1952, Grue and Jensen 1979, Klevesal' 1980). These factors likely vary on time and spatial scales, as well as among individuals, resulting in differences in the amount and timing of cementum deposition. Such variation in the deposition process may lead to some of the differences we observed among otters (i.e., 46 and

45; Fig. 3). Our observations suggest deposition may be most variable in the early years of growth and development and again as an animal becomes aged.

Protocols used when counting cementum deposits in sea otter teeth may be improved. Particular attention should be made in defining the criteria used to assign annuli to deposits made during the developmental years and in the oldest ages. None of the readers in this experiment had a catalog of known age sea otter premolar tooth sections from which to develop ageing criteria. The known age tooth samples acquired during this study can provide a valuable tool in further developing and refining the protocols used to define and count cementum deposits in the premolar teeth of sea otters. Although development of the method may be possible with the aid of the samples used in this study and additional readers, further testing of the readers used in this study will require additional known age specimens from wild sea otter populations that are difficult to obtain.

Accuracy of the method currently may be suitable for estimating age class distributions, or useful in estimating age specific demographic variables such as growth, survival or reproductive rates, based on relatively large sample sizes within age groupings. In our test, with experienced, although untested readers, 6–7 sea otters per age class closely approximated the known age distribution. However, until improvement in the accuracy of the technique can be demonstrated, age estimates of individual sea otters with cementum deposits potentially contain large errors and should be used with caution.

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