Marine Mammal Science

MARINE MAMMAL SCIENCE, 25(2): 478–486 (April 2009)

DOI: 10.1111/j.1748-7692.2008.00269.x

Ageing live ringed seals (*Phoca hispida*): Which tooth to pull?

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The count of growth layer groups (GLGs; Perrin and Myrick 1980) in tooth tissues to estimate pinniped ages is well established (Scheffer 1950; Laws 1952, 1962; Klevezal and Kleinenberg 1969; Hohn 2002). In the past, the canine has been the most commonly used tooth for age determination in pinniped studies because of its larger size and clarity of GLG (Laws 1953, McLaren 1958, Mansfield and Fisher 1960, Hewer 1964, Bowen *et al.* 1983). However, the canine cannot be removed from live animals due to the potential negative effects on foraging behavior (Arnbom *et al.* 1992, Childerhouse *et al.* 2004) and reproductive success. Incisors and post-canines can be quickly and humanely extracted from lightly sedated or anesthetized animals (Arnbom *et al.* 1992) and have been successfully used for age determination in a number of different pinniped species when a lethal technique was not scientifically or ethically appropriate (Antarctic fur seal, *Arctocephalus gazella*, and southern elephant seal, *Mirounga leonina*, Arnbom *et al.* 1992; grey seal, *Halichoerus grypus*, Bernt *et al.* 1996; crabeater seal, *Lobodon carcinophagus*, Laws *et al.* 2002; New Zealand sea lion, *Phocarctos hookeri*, Childerhouse *et al.* 2004; subantarctic fur seal, *Arctocephalus tropicalis*, Dabin *et al.* 2004; New Zealand fur seal, *Arctocephalus forsteri*, McKenzie *et al.* 2007). Due to the high variability in the visibility of layered structures between species, tooth tissues, tooth types, and preparation techniques, it is essential to test the validity of new ageing methods for each species individually (Johnston *et al.* 1987). In this study, we examined the precision and accuracy of using a post-canine or incisor tooth instead of the canine for age determination in ringed seals (*Phoca hispida*).

Ringed seal samples were collected in 2004 from Inuit subsistence harvests in the Hudson Bay communities of Arviat and Sanikiluaq, Nunavut, Canada. Jaws were simmered in hot water for two to three hours. Lower right canine (C, $n = 18$), first post-canine (PC1, $n = 20$) and second incisor (I2, $n = 20$) teeth were removed from the jaw bone and preserved in 70% ethanol. The periodontal ligament was not cleaned from teeth to prevent potential damage to the most recently deposited GLG. Decalcified, stained, longitudinal tooth sections were used and GLGs were read in the cementum following the technique described by Stirling *et al.* (1977), Bernt *et al.* (1996), and Stewart *et al.* (1996). However, incisors and post-canines were decalcified in a 2% nitric acid bath compared to 5% for canines. GLGs were counted in two to three blind replicates for each tooth type by one reader (MC). Final ages were estimated using two identical readings or the median of three different readings.

In the absence of known-age material, accuracy of age estimates was addressed through the difference observed between ages estimated using first post-canine and second incisor and ages estimated using canine teeth. Here, we assumed that ages determined by canine represented "true" age. Thus, the accuracy as defined above is termed "relative accuracy," hereafter. The precision was addressed using the precision index D (Chang 1982) defined as:

$$D = \sum_{i}^{n} CV_i / \sqrt{N_i} \qquad (1)$$

where CV is the coefficient of variation (standard deviation/mean) and N the number of readings for each individual i. A subjective measure of clarity of sections attributed to each tooth type for each seal was recorded for the second reading. Clarity indicated whether or not GLGs were clear and easy to count and was rated poor, medium, or good. This parameter could potentially influence the accuracy and the precision of final age estimates by reflecting the quality of the intrinsic layered structure of the tooth or the preparation techniques (Hohn *et al.* 1989, Stewart and Stewart 2005).

Data were not distributed normally (Shapiro–Wilk normality test; $P < 0.0001$) for all tooth types and all data sets: age estimates, relative accuracy, clarity and precision index, D, so non-parametric statistical tests were used. The effect of clarity on the relative accuracy and the precision was tested using a Kruskal–Wallis one-way analysis of variance test. Median of ages estimated for the three tooth types, as well as the precision index (D) were compared using Friedman two-way analyses of variance. The correlation between precision index D and number of GLGs was explored using a Spearman correlation. Tests for differences in frequency of clarity and relative accuracy for first post-canine and second incisor teeth were examined using chi-square. A quantile regression, using the 50% quantile or median, and Spearman correlation coefficients were used to investigate the relationship between ages estimated by first post-canines and second incisors and ages estimated by canines. Quantile regression is a robust statistic that circumvents limitations of least-square regression by not relying on assumptions of normality and homoscedascity and is relatively insensitive to outliers (Koenker 2005). Standard errors and t-ratios were estimated using 1,000 bootstrap samples. Standard errors of estimates were computed using the median regression coefficients as follow:

$$S_{Y,X} = \sqrt{\sum_{i}^{n} (Y_i - Y_i')^2 / n - 2} \qquad (2)$$

where Y' is the estimated value of Y for each individual i and n is the sample size.

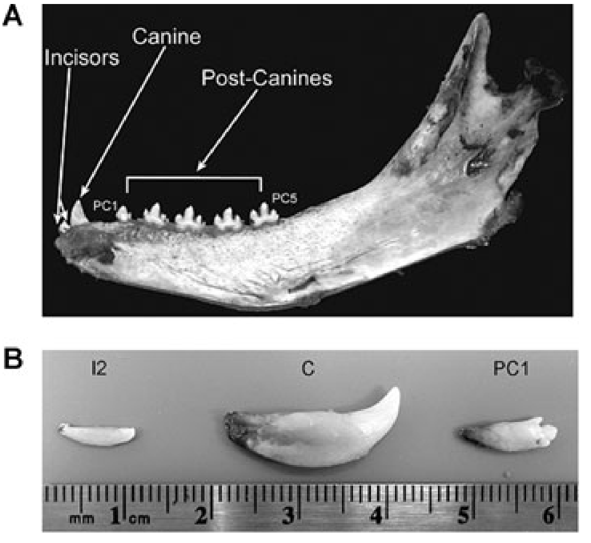

Figure 1. (A) Lingual aspect of an adult ringed seal right mandible and location of the different teeth; (B) relative size of the three tooth types considered in this study in an adult ringed seal. I2: second incisor; C: canine; PC1: first post-canine.

Statistical analyses were performed using Systat 11 software (SPSS Inc., Chicago, IL) and the GNU R system (http://www.r-project.org/). Unless otherwise stated, results are provided as mean ± standard deviation (SD). Differences were considered significant at $P < 0.05$.

The first post-canine and the second incisor are both characterized by a single root (Fig. 1) and should be relatively easy to extract from a live ringed seal, as observed for other species (Arnbom *et al.* 1992, Bernt *et al.* 1996, Childerhouse *et al.* 2004, Dabin *et al.* 2004, McKenzie *et al.* 2007). Although both are about the same length in ringed seal, the first post-canine is thicker and wider than the second incisor (Fig. 1), and was therefore easier to manipulate during the decalcification, sectioning, and mounting processes. This difference was particularly significant during the sectioning stage when the tiny incisor sections rolled-up on themselves and were consequently at risk of loss and more difficult to mount without damage. Choosing the best sections to mount among curled sections was also challenging. In contrast, obtaining mid-longitudinal sagittal sections from the ringed seal first post-canines was more difficult than for incisors and canines because they are curved in two directions and present a "lump" on one side, making it difficult to cut the pulp cavity through the center. Adjustments of the tooth position relative to the blade during the sectioning stage provide the right alignment for mid-longitudinal sagittal sections. Although the relative large size of the pulp cavity in canines did allow for these adjustments before the center of the cavity was reached, the smaller size of the pulp cavity in both first post-canines and incisors prevented them. GLGs in offset sections can be confusing to interpret, which in turn could affect precision and relative accuracy (Hohn *et al.* 1989).

In ringed seals, all permanent teeth have erupted at the time of, or shortly after, birth (Stewart *et al.* 1998), suggesting a concomitant and early cementum deposition

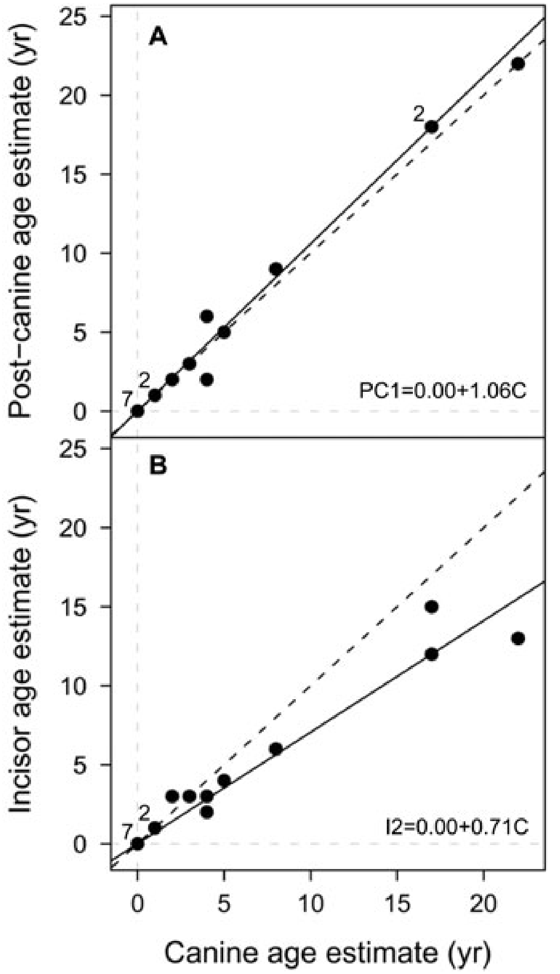

Figure 2. Median regression (solid lines) of ringed seal (a) first post-canine age estimates $n = 18$, $r_s = 0.99$, $S_{YX} = 0.80$ and (b) second incisor age estimates $n = 18$, $r_s = 0.98$, $S_{YX} = 1.12$, on canine age estimates. Dashed black lines represent the $y = x$ regression; dashed light gray lines indicate the zero for x- and y-axis; n is the sample size; r_s is the Spearman correlation; S_{YX} is the standard error of estimates; the number of seals represented by a particular dot is specified beside the dot, if superior to one. I2: second incisor; C: canine; PC1: first post-canine.

and therefore a complete representation of the growth pattern for both second incisor and first post-canine teeth (Morris 1972). In this study, high correlations were found between ages estimated by canine, first post-canine, and second incisor (Fig. 2), corroborating the hypothesis of a similar growth pattern in the cementum of the three tooth types in ringed seals. However, the canine and first post-canine of three ringed seals aged as pups (0 yr) had some cementum whereas no cementum was recorded in the second incisor of the same individuals. The cementum was generally thinner in the second incisor compared to the first post-canine of the same animal. As

Table 1. Comparison of clarity of sections (n = 20) and relative accuracy of ages (n = 18) obtained from ringed seal first post-canine and second incisor teeth. Achieved/Underest./Overest.: ages estimated by counting GLGs in the post-canine or the incisor cementum match/underestimate/overestimate ages estimated with the canine.

	Clarity (%)			Relative accuracy (%)		
	Poor	Medium	Good	Achieved	Underest.	Overest.
First post-canine	50	25	25	72.2	5.6	22.2
Second incisor	55	15	30	55.5	38.9	5.6
P (χ^2)		0.2			*0.03*	

a result, GLGs in the wider cementum of post-canines were generally more widely spaced and easily counted and interpreted compared to GLGs in incisors. Both tooth types, however, had less cementum than canines. Counting GLGs in the root (apical end) was compromised in first post-canine and second incisor teeth because of compressed GLGs and thin cementum deposition, respectively. The position of the first post-canine in the mandible (*i.e.*, adjacent to the canine and above its root) may limit the space available in the socket for the cementum to grow. In second incisors, the cementum often presented involutions along sides and near the root area compromising GLGs counts and interpretation. The edge effect created by stain at the interface of the cementum with the periodontal ligament was generally more pronounced in first post-canines and second incisors, compared to canines. Therefore, the last deposited cementum layer may be harder to distinguish in these tooth types.

Ages estimated by counting GLGs in canine, first post-canine, and incisor were different (Friedman ANOVA: $\chi^2 = 6.929$, df $= 2$, $P = 0.031$). The median regressions of first post-canine and second incisor on canine age estimates showed a positive relationship (PC1: $t = 3.843$, $P = 0.001$; I2: $t = 3.197$, $P = 0.005$), with intercepts not different from 0 (PC1: SE $= 1.620$, $P = 1$; I2: SE $= 1.545$, $P = 1$) but a slope not different from 1 only for first post-canine (PC1: SE $= 0.275$, 95% CI $= 1.000$–1.064; I2: SE $= 0.221$, 95% CI $= 0.578$–0.882; Fig. 2). These results suggested that relative accuracy improved when GLGs were counted in the first post-canine cementum relative to the second incisor. The latter tended to underestimate canine age (Table 1) and was less reliable, especially for older animals (Fig. 2). Indeed, the standard error of the estimate, a measure of accuracy (Dapson 1980), was larger when the second incisor was the dependent variable compared to first post-canine (Fig. 2). The difference in mean age between canine age was -1.16 yr for the second incisor similar to the differences in age found by Bernt *et al.* (1996), compared to 0.16 yr for first post-canine. This discrepancy was largely due to a higher proportion of differences $\geq$2 yr when reading the incisor (28%) relative to the post-canine (11%), and in particular due to two incisor age estimates that underestimated the canine age by 5 and 9 yr. Canine ages corresponding to these two outliers were 18 and 22 yr old, respectively, indicating that in the second incisor of older seals, GLGs are overcrowded due to thin cementum deposition later in life, compromising accurate reading for age estimation. Of the five post-canines that departed from canine age estimates, three were from adult ($\geq$6 yr) and two from juvenile seals. One ringed seal would have been mistakenly classified as sexually mature based on first post-canine age (6 yr old compare to 4 yr old based on canine age). Notes taken while blindly reading the above-mentioned incisor and post-canine sections confirmed the extreme difficulty in distinguishing and counting the GLGs. Three readings were required and the median was used to determine final age estimates with a resulting precision index greater (*i.e.*, less precision achieved) than the mean. Overall departure from canine ages was not greater than 2 yr for 100% and 75% for first post-canine and second incisor, respectively. For both tooth types, relative accuracy was higher in 0- and 1-yr-old individuals (100%) than seals $\geq$2 yr (PC1: 44%; I2: 11%). This result agrees with previous studies (Anas 1970, Bowen *et al.* 1983, Lawson *et al.* 1992, Bernt *et al.* 1996). The relative accuracy we recorded for first post-canine and second incisor (Table 1) was in the range of accuracy described in the literature for other seal species (Arnbom *et al.* 1992, Antarctic fur seal first post-canine: 82.6%; Bernt *et al.* 1996, grey seal incisor: 58.8%; Childerhouse *et al.* 2004, New Zealand sea lion first post-canine: 39%; McKenzie *et al.* 2007, New Zealand fur seal first post-canine: 77.3%).

The precision index (D) calculated in this study (C: 0.128 $\pm$ 0.321, PC1: 0.102 $\pm$ 0.244, I2: 0.055 $\pm$ 0.137) was not different among the three tooth types (Friedman ANOVA: $\chi^2 = 0.182$ df = 2; $P = 0.913$) and agreed with results of Albright (1990) for canines (0.0415–0.1342) from ringed seals using the same ageing method (longitudinal, stained sections). Assuming each tooth was carefully examined before being positioned for sectioning to obtain good mid-longitudinal sagittal sections and that D represented a good measure of precision, this result suggested differences in size, shape, cementum thickness and deposition pattern among post-canines and incisors did not play a major role in the repeatability of GLGs counts in ringed seal teeth. A pattern of decreasing precision (increasing variance) with increasing number of GLGs (Johnston *et al.* 1987, see Evans *et al.* 2002) or no relationship (Evans *et al.* 2002) has been reported. In this study, we found a significant negative correlation between the precision index, D, and GLG number for the second incisor ($r_s = 0.469$, df = 18, $P = 0.037$), but the trend was not significant for the canine ($r_s = 0.041$, df = 16, $P = 0.871$) nor the post-canine ($r_s = 0.354$, df = 18, $P = 0.126$). From our results, and in contrast to previous studies, it appeared that the repeatability in reading the GLGs tended to be better for older animals compared to zero, 1- and 2-yr age classes. However, teeth from older seals, and especially post-canines and incisors, more commonly required three compared to two replicate readings (mean age for two readings: C: 4.154 $\pm$ 7.093 yr; PC1: 1.818 $\pm$ 2.892 yr; I2: 2.143 $\pm$ 2.983 yr; mean age for three readings: C: 5.6 $\pm$ 7.021 yr; PC1: 11 $\pm$ 9.394 yr; I2: 8.5 $\pm$ 8.264 yr). Although caution in interpretations is required due to our small sample size (especially for animals older than 10 yr of age, which represented 17% of the sample), the ambiguity of results presented above could be an artifact of how the precision index was calculated. Small deviations from the mean in young animals will result in lower precision (higher precision index) than the same deviation in older animals (Albright 1990). Indeed, a tooth section read three times with two readings differing by 1 yr will result in a precision index of 0.014 and 0.5 for a 24-yr-old and a 1-yr-old seal, respectively. Our results called for caution in using the index D for precision in age estimation techniques.

Clarity of sections was rated "good" for 25% and 30% of first post-canines and second incisors respectively (Table 1) and did not affect the "relative accuracy" (Kruskal–Wallis ANOVA: PC1: $\chi^2 = 0.099$, df = 2, $P = 0.952$; I2: $\chi^2 = 4.033$, df = 2, $P = 0.133$), nor the precision in canines and post-canines (Kruskal–Wallis ANOVA: C: $\chi^2 = 2.436$, df = 2, $P = 0.296$; PC1: $\chi^2 = 0.883$, df = 2, $P = 0.643$). However, the least precise incisor sections were all associated with a poor clarity index (Kruskal–Wallis ANOVA: $\chi^2 = 6.396$, df = 2, $P = 0.041$). This result suggests that second incisor sections were more difficult to read than canine or post-canine sections. This is most likely due to smaller size of incisors and the relatively greater effect off-set sections could potentially have on GLGs interpretation (Hohn *et al.* 1989).

Our results should be interpreted relative to possible study limitations. The relatively small sample size prevented testing for effects due to sex and geographic location. Sex has been previously reported to influence the accuracy and precision of age estimates, GLGs from females being more difficult to interpret than GLGs from males (Laws 1953, Anas 1970, Scheffer and Myrick 1980, Schiavini *et al.* 1992, Stewart *et al.* 1996, Molina-Schiller and Pinedo 2004, Stewart and Stewart 2005). The effect of geographic location on repeatability of age estimates has been suggested by Albright (1990). In this study, the sex ratio of our sample was 1:1 and the two Hudson Bay communities (Arviat and Sanikiluaq) were represented equally (although, two canines had to be removed from the Arviat sample after the decalcification process). The annual deposition of GLGs in ringed seals still needs to be validated using known-age animals. In this study, we compared ages obtained from first post-canine and second incisor to ages obtained from canine and calculated a "relative" accuracy. By doing so, we assumed that ages estimated by reading GLGs in canine teeth represented "true" ages and were thus error-free, which is not likely the case. The experience and training of readers can be a source of variability in the determination of age estimates (Anas 1970, Albright 1990, Lawson *et al.* 1992, Bernt *et al.* 1996, Evans *et al.* 2002). Between-reader variations in relative accuracy and precision were not a factor in our study because only one person did all the readings.

In conclusion, we recommend preferentially extracting the first post-canine versus the second incisor in live ringed seals due to (1) larger size and cementum deposition, (2) greater ease of manipulation during the different steps of tooth preparation for ageing, and (3) greater relative accuracy.

Acknowledgments

We thank the Arviat Hunters and Trappers Organization, the Sanikiluaq Hunters and Trappers Association, Frank Nuturasungnik, Lucassie Ippak, Lucassie Takatak, and hunters from the communities of Arviat and Sanikiluaq, Nunavut, Canada, for providing seal samples. Drs. M. Hammill and I. Stirling warmly welcomed MC in their respective laboratories. Jean-Francois Gosselin, Richard Labbé and Cheryl Spencer provided valuable advice and support during the process of learning ageing procedures. Sebastián Luque provided useful comments and help with the use of the GNU R system. The manuscript was improved thanks to comments from Dr. R. E. A. Stewart and three anonymous reviewers. Seal sample collections were conducted under Fisheries and Oceans Canada License to fish for scientific purposes. This research was funded by Fisheries and Oceans Canada, Manitoba Hydro, University of Manitoba, ArcticNet, and the Nunavut Wildlife Management Board.

Literature Cited

Albright, D. M. 1990. A critical evaluation of age determination of ringed seals (*Phoca hispida*, Schreber 1775). M.Sc. thesis, MacDonald College of McGill University, Montreal, Quebec, Canada. 118 pp.

Anas, R. E. 1970. Accuracy in assigning ages to fur seals. Journal of Wildlife Management 34:844–852.

ARNBOM, T. A., N. J. LUNN, I. L. BOYD AND T. BARTON. 1992. Aging live Antarctic fur seals and southern elephant seals. Marine Mammal Science 8:37–43.

BERNT, K. E., M. O. HAMMILL AND K. M. KOVACS. 1996. Age estimation of grey seals (*Halichoerus grypus*) using incisors. Marine Mammal Science 12:476–482.

BOWEN, D. W., D. E. SERGEANT AND T. ØRITSLAND. 1983. Validation of age estimation in the harp seal, *Phoca groenlandica*, using dentinal annuli. Canadian Journal of Fisheries and Aquatic Science 40:1430–1441.

CHANG, W. Y. B. 1982. A statistical method for evaluating the reproducibility of age determination. Canadian Journal of Fisheries and Aquatic Science 39:1208–1210.

CHILDERHOUSE, S., G. DICKIE AND G. HESSEL. 2004. Ageing live New Zealand sea lions (*Phocarctos hookeri*) using the first post-canine tooth. Wildlife Research 31:177–181.

DABIN, W., G. BEAUPLET, E. A. CRESPO AND C. GUINET. 2004. Age structure, growth, and demographic parameters in breeding-age female subantarctic fur seals, *Arctocephalus tropicalis*. Canadian Journal of Zoology 82:1043–1050.

DAPSON, R. W. 1980. Guidelines for statistical usage in age-estimation techniques. Journal of Wildlife Management 44:541–548.

EVANS, K., M. A. HINDELL, K. ROBERTSON, C. LOCKYER AND D. RICE. 2002. Factors affecting the precision of age determination of sperm whales (*Physeter macrocephalus*). Journal of Cetacean Research and Management 42:193–201.

HEWER, H. R. 1964. The determination of age, sexual maturity, Longevity and a life-table in the grey seal (*Halichoerus grypus*). Proceedings of the Royal Society of London 142:593–624.

HOHN, A. A. 2002. Age estimation. Pages 6–13 *in* W. F. Perrin, B. Würsig and H. G. M. Thewissen, eds. Encyclopedia of marine mammals. Academic Press, San Diego, CA.

HOHN, A. A., M. D. SCOTT, R. S. WELLS, J. C. SWEENEY AND A. B. IRVINE. 1989. Growth layers in teeth from known-age, free-ranging bottlenose dolphins. Marine Mammal Science 5:315–342.

JOHNSTON, D. H., D. G. JOACHIM, P. BACHMANN, K. V. KARDONG, R. E. A. STEWART, L. M. DIX, M. A. STRICKLAND AND I. D. WATT. 1987. Aging furbearers using tooth structure and biomarkers. Pages 229–243 *in* M. Novak, J. A. Baker, M. E. Obbard and B. Malloch, eds. Wild furbearer management and conservation in North America. Ministry of Natural Ressources, Ontario, Canada.

KLEVEZAL, G. A., AND S. E. KLEINENBERG. 1969. Age determination of mammals by layered structure in teeth and bone. D. E. Sergeant, ed. Fisheries Research Board of Canada, Translation Series 1024, Arctic Biological Station, Ste. Anne de Bellevue, Quebec, Canada. 142 pp.

KOENKER, R. 2005. Quantile regression. Cambridge University Press, Cambridge, UK.

LAWS, R. M. 1952. A new method of age determination for mammals. Nature 169:972.

LAWS, R. M. 1953. A new method of age determination in mammals with special reference to the elephant seal (*Mirounga leonina, Linn.*). Falkland Islands Dependencies Survey, Scientific Reports 2. 11 pp.

LAWS, R. M. 1962. Age determination in pinnipeds with special reference to growth layers in the teeth. Zeitschrift für Säugetierkunde 27:129–146.

LAWS, R. M., A. BAIRD AND M. M. BRYDEN. 2002. Age estimation in crabeater seals (*Lobodon carcinophagus*). Journal of Zoology of London 258:197–203.

LAWSON, J. W., G. D. HARRISON AND D. W. BOWEN. 1992. Factors affecting accuracy of age determination in the harp seal, *Phoca groenlandica*. Marine Mammal Science 8:169–171.

MANSFIELD, A. W., AND H. D. FISHER. 1960. Age determination in the Harbour seal, *Phoca vitulina* L. Nature 186:92–93.

MCKENZIE, J., B. PAGE, P. D. SHAUGHNESSY AND M. A. HINDELL. 2007. Age and reproductive maturity of New Zealand fur seals (*Arctocephalus forsteri*) in Southern Australia. Journal of Mammalogy 88:639–648.

MCLAREN, I. A. 1958. The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctic. Fisheries Research Board of Canada, Bulletin 118. 97 pp.

MOLINA-SCHILLER, D., AND M. C. PINEDO. 2004. Growth layer patterns in *Arctocephalus australis* canine teeth: Evaluation of techniques for age determination. Latin American Journal of Aquatic Mammals 3:107–118.

MORRIS, P. 1972. A review of mammalian age determination methods. Mammal Review 2:69–104.

PERRIN, W. F., AND A. C. J. MYRICK. 1980. Age determination of toothed whales and sirenians. Report of the International Whaling Commission (Special Issue 3):1–218.

SCHEFFER, V. B. 1950. Growth layers on teeth of pinnipedia as an indicator of age. Science 112:309–311.

SCHEFFER, V. B., AND A. C. J. MYRICK. 1980. A review of studies to 1970 of growth layers in the teeth of marine mammals. Report of the International Whaling Commission (Special Issue 3):51–63.

SCHIAVINI, A. C. M., M. LIMA AND L. M. BATALLES. 1992. Growth structures of maxillary canines of the southern fur seal (*Arctocephalus australis*). Marine Mammal Science 8:89–93.

STEWART, R. E. A., AND B. E. STEWART. 2005. Comparison of between-tooth age estimates of Atlantic walrus (*Odobenus rosmarus rosmarus*). Marine Mammal Science 21:346–354.

STEWART, R. E. A., B. E. STEWART, I. STIRLING AND E. STREET. 1996. Counts of growth layer groups in cementum and dentine in ringed seals (*Phoca hispida*). Marine Mammal Science 12:383–401.

STEWART, B. E., S. INNES AND R. E. A. STEWART. 1998. Mandibular dental ontogeny of ringed seals (*Phoca hispida*). Marine Mammal Science 14:221–231.

STIRLING, I., W. R. ARCHIBALD AND D. DEMASTER. 1977. Distribution and abundance of seals in the Eastern Beaufort Sea. Fisheries Research Board of Canada 34:976–988.

Received: 17 March 2008
Accepted: 16 September 2008