A Critical Evaluation of Age Determination of Ringed Seals (*Phoca hispida* Schreber 1775)

by

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Variance in Age Determination

Abstract

Precision of determining age in ringed seals (*Phoca hispida*) was examined by repeated readings of undecalcified cross sections and decalcified stained longitudinal sections of mandibular canines. There appeared to be geographical differences in repeatability although this could not be tested statistically. There was no difference in repeatability between cross and stained sections.

The effect of precision on population parameters was examined. Smoothing procedures necessary to construct life tables and to do Leslie matrix calculations obscured any differences in ages between readings. Variance between readings was found to give inconsistent notions of sexual maturity. Imprecision caused little overall difference in growth curves.

Without known age animals, accuracy can not be evaluated directly. High correlation between ages from canines from different sides of the same animal, between dentine and cementum of teeth from the same animal, and between readers examining the same sets of teeth gave an indirect suggestion of accuracy.

Resume

On a examiné la précision de la détermination d'age chez le phoque annelé (*Phoca hispida*) par des lectures répetées de coupes transversales non décalcifiées et de coupe teintées longitudinales décalcifiées de canines mandibulaires. Il semble y avoir des différences géographiques notables dans la répétition des lectures quoique cela n'a pu être vérifié statistiquement. On a observé aucune différence dans la répétition entre les coupes transversales et teintées.

On a aussi examiné dans cette étude, l'effect de la précision sur les paramètres démographiques. Les techniques de lissages pré requises à l'élaboration des tables de vie et aux calculs matriciels de Leslie ont masqué toute différence d'age entre les lectures. On a constaté que la variance inter lecture générait des notions contradictoires sur la maturité sexuelle de individus. L'imprécision rencontrée au cours des lectures n a causé que des différences minimes globales dans les courbes de croissance.

La fidélité dans les lectures ne peut être évaluée directement sans avoir des spécimen d'age connus. De fortes corrélations ont été observées entre les ages de canines de différent côté de l'animal, entre la dentine et

le ciment des dents du meme animal et entre les lectures avant examiné la meme série de dents et sont indirectements suggestives de la fidélite.

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Thesis Office Statement

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PREFACE

The literature on determining age of animals is voluminous. Techniques range from absolute determinations such as recapture of animals marked when they were young (e.g. Stirling 1971) to such esoteric, indirect methods as relative brittleness of tail collagen at different ages (Sherman et al. 1985). Cain (1962) furnishes a bibliography on various methods of age determination. A more recent review is provided by Morris (1972).

Determining age of animals from structures on the tooth surface or within the tooth was established in the early 1950s by Scheffer (1950) and Laws (1952). Originally developed in pinnipeds, use of the technique quickly spread to other species. Morris (1978) and Fancy (1980) review determination of age from dental structures in general.

Klevezal and Kleinenberg (1967) review age determination from teeth and bones in nine orders. Spinage (1973) concentrates on use of the technique in African mammals. Grue and Jensen (1978) provide a résumé of age determination from cementum of various terrestrial species. Perrin and Myrick (1980) focus on use of layers in teeth and bones of odontocetes.

McLaren (1958) pioneered age determination of ringed seals (*Phoca hispida*) from the dentine of canine cross sections. Tikhomirov and Klevezal (1964) and Smith (1973) published lengthy descriptions of tooth structure and discussions on age determination from dentine of cross sections. All these authors agree the neonatal line is visible in the dentine of cross sections cut from the region below the enamel cap. Counts to determine age begin at the neonatal line and include an opaque and a transparent incremental growth layer (IGL; Myrick 1980) in each growth layer group (GLG; Myrick 1980). However McLaren (1958) and Tikhomirov and Klevezal (1964) mention vacuolated (or interglobular or reticulated) dentine as being more extensive than does Smith (1973).

Tikhomirov and Klevezal (1964) remark that IGLs can be seen in cementum of histologically prepared, longitudinal sections. However they preferred cross sections because of ease of preparation. Stirling et al. (1977) are to my knowledge the first to count cemental layers of ringed seals. While Helle (1975) utilized dentine in cross sections, later he (Helle 1979) used cementum from decalcified, stained longitudinal sections to determine age. Lydersen and Gjertz (1987) also use cementum.

There are many advantages of using teeth to determine age. This technique can be used in short term studies of long-lived animals or where tag-recapture methods are not feasible. Other techniques of age determination, e.g. appearance of pelage or length, can also be used in these cases but give only a relative age. The biggest advantage of determining age from dental structures is that it gives discrete ages which establish age specific parameters for population modelling.

The advantage of discrete ages gained by counting dental layers seems to have blinded early proponents to potential problems with the technique. For example, Laws (1953) used dentinal layering to determine age of southern elephant seals (Mirounga leonina) but it was a decade before Carrick and Ingham (1962) tested accuracy by comparing read ages to known ages of tagged animals.

Not only has the subject of accuracy been ignored, so has the question of precision. Recently there has been increasing recognition that reproducibility (see Glossary) may have an effect on age determination among readers (Perrin and Myrick 1980; ICES 1986).

While increasing numbers of researchers report measures of precision (e.g. Daniels 1983; Sikstrom 1983; Prince et al. 1985; van Aarde 1985; McGowan et al. 1987; Galbraith and Brooks 1989) there has been little consideration of the effect precision may have on perceptions of the status of populations. With this in mind I studied the precision in age determination from teeth of ringed seals. More importantly I looked at the effect this precision had on estimates of population parameters.

The ringed seal was chosen as a model for several reasons. The large collection of teeth from this species held at the Arctic Biological Station (Department of Fisheries and Oceans) was made available, so sample size was not a problem. These teeth were from a number of areas so geographic differences could be examined.

Although the European Economic Community's ban on seal skin imports has curtailed the harvest, ringed seal populations will continue to be monitored and managed (Stewart et al. 1986). Ringed seals still form an important part of northern people's diet (Alton Mackey and Orr 1987), and pressure on the resource will increase as the Inuit population expands (Bliss et al. 1973; Davis 1981). The ringed seal is also an important prey item for polar bears (Ursus maritimus). It is estimated the 2000 bears in the Alaskan Beaufort Sea consume 146,000 ringed seals annually (B.P. Kelly, S.C. Armstrup, C. Gardner, and L.T. Quakenbush. 1987. Predation on ringed seals in the western Beaufort Sea. Poster at Seventh biennial conference on the biology of marine mammals, Miami, Florida, Dec. 5-9, 1987). The International Agreement on the Conservation of Polar Bears and their Habitat requires the five signing nations to protect the ecosystems of which polar bears are a part (Stirling 1986). Thus managing ringed seals could indirectly fall under this agreement.

Ringed seals are used to study the distribution and bioaccumulation of pollutants because of their position in the trophic web (Wagemann 1989). Smith and Hammill (1989) suggest ringed seals may be used as indicator species of regional changes in arctic marine production. Questions relating to changes which occur under the influence of exploitation and release from exploitation (Ohsumi 1986) or increased or decreased food resources (Bengtson and Laws 1985) might profitably be looked at in ringed seals. These questions require a repeatable method of age determination.

Although hydrocarbon exploration in the arctic is currently reduced, development will eventually become economically feasible. Continuing long term studies are necessary so impact studies and amelioration can be based on reliable information rather than on ad hoc short term studies (Davis 1981). Presently there is a pilot project using seal oil to dilute heating fuel in Pelly Bay, N.W.T.

(Anonymous 1988). If this is successful, ringed seals will be a major source of oil because of their ubiquity. For all the above reasons it is obvious age determination of ringed seals is of practical importance as well as scientific interest.

As permitted by the Faculty of Graduate Studies this thesis includes the text of two manuscripts which are to be submitted to the Canadian Journal of Fisheries and Aquatic Sciences with Dr. T.G. Smith as co-author. The first manuscript quantifies the amount of precision and examines the effect of precision on various commonly calculated population parameters. The second manuscript comments on the accuracy of using laminations in teeth to determine age.

I carried out the collection and analysis of data and writing of the manuscripts. Two other people also read tooth sections for me. Mike Hammill provided access to measurements from the Barrow Strait seals.

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SECTION I

Precision of age determination in ringed seals (*Phoca hispida*) and its effect on calculation of population parameters

Knowledge of age structure underlies most of our understanding of population dynamics and attempts at managing animal populations. Age determination techniques using length or weight of animals give relative ages with arbitrary, broad categories (Morris 1978). They cannot provide information on population parameters such as reproductive and mortality rates, time to sexual maturity, and longevity.

Marking and recapture of animals give direct estimates of age. However not all species are amenable to this method. For example, ringed seals (*Phoca hispida*) are solitary animals inhabiting an environment which is difficult to work in, making the probability of returns from tagging experiments low (Smith 1987). In such cases and in short term studies of long-lived animals it is necessary to find a physical feature which records the age of individual specimens. In most mammals, layering in dentine or cementum of teeth is used.

Sych's (1974) model was modified to conceptualize the process of age determination (Figure 1). The age of the animal is encoded in a hard structure. This information is viewed using an imaging system and the observer perceives and processes the information, comparing it to a prototype fixed in memory (Wickelgren 1981). The final step is the output of the information when the reading is recorded. Accuracy and precision act on different parts of this communication channel. Problems of accuracy result from the coding of information in the teeth while problems of precision result from perception and processing of this information.

Accuracy and precision are recognized as different in this model and in the field of statistics. Accuracy is the closeness of the coded information to its true value. Precision is the consistency with which repeated readings arrive at the same output. Since the two processes are separate, coding in a structure might exist but be so unclear that consistent perception is not possible. It is also possible the coded information is inaccurate but highly repeatable. Furthermore it is possible to analyze one source of error without direct knowledge of the other.

Age of the ringed seal is coded as a series of transparent and opaque incremental growth layers (IGLs; Myrick 1980). McLaren (1958) determined an opaque and a transparent IGL are laid down over a year in the life of the ringed seal, thereby forming a growth layer group (GLG; Myrick 1980). However "transparent" and "opaque" are relative terms (Klevezal and Kleinenberg 1967) and growth layers are not restricted to these two categories but may assume intermediate opacities. Furthermore, Klevezal and Sukhovskaya (1983) make the point that perceived opacity of a layer will be influenced by opacity of the layers adjacent to it. Assignment of many of the IGLs to either classification becomes subjective.

Readings of teeth will be affected by: (1) level of experience, which affects the observer's ability to repeatedly distinguish transparent and opaque IGLs; (2) the reader's ability to keep his place when counting, i.e. to not get "lost" among the GLGs and double count some and miss others; (3) the reader's state of mind, e.g. motivation, fatigue, emotional state; (4) distractions from outside sources; (5) type of preparation, e.g. unstained, undecalcified cross sections; decalcified, stained longitudinal sections. All these factors combine to give variation in interpretation by the same observer at different times (Nellis et al. 1978; Payne 1978; Hamilton 1982; Hillman-Smith et al. 1986) or by different observers (Kimura 1980; Boehlert 1985; Hillson 1986; Jean et al. 1986).

I and other workers inspected the same set of teeth repeatedly to explore the question of how reproducible age determination of ringed seal is. I then evaluated the effect of imprecision in age determination on estimates of population parameters.

MATERIALS AND METHODS

Preparation of materials

Cross, also called horizontal or transverse, sections were cut from the lower canine of ringed seals and examined from more than 700 specimens from Amundsen Gulf (Holman), 132 specimens from Barrow Strait (Resolute), and 106 specimens from Svalbard (Figure 2) by myself (Reader 1). This was my first experience in age determination from dental structures. A subsample of 50 was selected from the 1981 Holman teeth, for reading by an observer with several years experience (Reader 2). Ages of 48 Resolute teeth were determined by another worker (Reader 3), as well. This reader was experienced in age determination from cementum in histological sections, but this was his first attempt at reading undecalcified cross sections. After 3 to 5 readings he consulted my age readings then made another 3 or 4 readings of the sections. Thus I have "naive" and "experienced" readings from him.

Cross sections were taken from the area just below the enamel cap as this location is repeatable between teeth (Jean et al. 1986) and the neonatal line should be visible (Smith 1973). Cross sections were cut on a custom built saw at the Arctic Biological Station (ABS), Ste-Anne de Bellevue, Quebec. A stream of cold tapwater prevented burning of the sections and cleaned dust from the kerf. Sections were 0.24±0.10 mm (mean±s.d., n = 30, range = 0.10-0.55 mm) thick and did not require polishing after cutting.

Histological sections prepared from a subsample of Holman and Resolute teeth for which there were also cross sections, were decalcified in 10% formic acid, sectioned on a cryostat, and stained with either haemaleum or 0.032% toluidine blue (C.I. 52040) (Table 1). The Holman sections had been prepared by a technician at ABS before this study began, but I decalcified and cut the Resolute teeth. Reader 3 stained these teeth.

Examination of undecalcified and decalcified preparations were made with transmitted light, reflected by a mirror through the specimen, using a stereo binocular dissecting microscope, generally at 25X magnification. At this magnification the whole section could be seen, so IGLs could be followed around the section. Narrow IGLs were examined at 50X when necessary. In most cases a Wild M5 was used, but while that microscope was being repaired, a Zeiss was used.

Each sample, whether cross or longitudinal, was inspected 7 times without reference to other biological data (Marsh 1980b). Cross sections were stored in labelled vials and kept in boxes. Teeth from each box were read randomly without reference to previous readings. Reading sessions lasted about 2 hours and were held in the morning and afternoon of most days. In this way re-examination of a particular section was separated by examination of a number of other teeth, reducing bias from memory as much as possible. Slides of stained sections were treated similarly but the smaller sample size meant re-examination of a particular tooth was closer together in time.

Counts of IGLs in the dentine of cross sections began at the neonatal line and an opaque then a transparent IGL was counted as a GLG (McLaren 1958; Tikhomirov and Klevezal 1964; Smith 1973). Counts of dentine in histological sections likewise began at the neonatal line and counted a wide, light-staining lamination and a narrow, dark-staining layer as a GLG. GLGs in the cementum of stained sections were considered to begin at the cemento-dentinal interface and to consist of a wide lightly stained IGL and a narrow darkly stained IGL, in common with several other species (e.g. Heggberget 1984; Mason 1984; and others).

If only the first opaque layer was visible the animal was recorded as 0+ GLGs and subsequently reported as age=0. Correspondingly, 1+ GLGs refers to an animal that is in the time interval between age 1 and age 2 (Ricker 1969). Such an animal would be recorded as age=1.

Data Analysis

Not all teeth had 7 age estimates available for analysis. Sections might be inadvertently missed during a particular reading session. For various reasons, e.g. the occurrence of osteodentine (clear areas without IGLs) near the pulp cavity, occasionally only a minimum age could be established. In such cases the reading was not included in the analysis. Arbitrarily, 5 readings were judged to be the minimum number necessary so any tooth with > 2 missing values was eliminated.

Various measures of precision were calculated. Following Beamish and Fournier (1981) average error (AE) and derived values were calculated:

$$\text{Average error (AE)} = \Sigma((X_{ij}-X_j)/X_j)/R$$

$$\text{Average percent error (APE)} = 100(\text{AE})$$

$$\text{Index of average error (IAE)} = \Sigma\text{AE}/N$$

$$\text{Index of average percent error (IAPE)} = 100(\text{IAE})$$

where:

R = number of times each section was examined;

X_{ij} = i^{th} age determination of j^{th} section;

X_j = average age calculated for the j^{th} section;

N = total number of specimens examined.

Coefficient of variati . (V):

$$V = \sigma / X_j$$

and an index of precision (D) (Chang 1982):

$$D = V/\sqrt{R}$$

were also calculated. For each reading, mean age of the resulting age distribution (X_i) was calculated:

$$X_i = \Sigma X_{ij}/N.$$

The Friedman test (Conover 1980) was used to test for differences among indices of precision (D) for cross sections and stained histological sections and between readers. Since D is positively correlated with the other measures (AE and V) (Chang 1982) the results are representative for them as well. Since the Friedman test is a rank test it is unaffected by differences in magnitude between the measures of precision.

Consequences of imprecision on population parameters were examined in several ways. Levene's test (Snedecor and Cochran 1980) showed there was homogeneity of variance between replicates so untransformed data was used in a one-way ANOVA to test for differences in individual age determinations (X_{ij}) among replicates.

The Friedman test was also used to examine if there was a difference in X_1 among Reader 1's replicates. This test requires a complete design so any readings with missing values were eliminated, thereby reducing sample size. Where significant differences were found, multiple comparison at $\alpha=0.05$ was performed.

To examine the effect of variance in age determinations on population projections, the frequencies from each of my 7 readings and their mean were smoothed. A first order linear regression was fit to a semi-log plot of frequency against age in years, excluding 0 age animals (Smith 1973). The number of 0 age seals was calculated from the smoothed age distribution multiplied by age-specific fecundities from Smith (1987). Twenty-two age-classes (ages 0-21) were included in the analysis. A BASIC language program was written which calculated life tables (Caughley 1977). Smith's (1970) Program F was translated to BASIC and used to arrive at a stable age distribution for each of the 8 age distributions.

Between reader effects could be examined because Reader 2 had also read the complete set of Holman teeth. For those animals read by both readers 1 and 2, I used X_1 from my 7 readings and the age from Reader 2's single reading. Each age frequency distribution was smoothed as above and a stable age distribution calculated.

If the imprecision in age determination is normally distributed and unbiassed, it should cancel itself out and have little effect on parameters calculated from different replicates of the same set of teeth. To examine whether differences in age determination was enough to affect the mean age of sexual maturity (ASM) a stochastic model was used. Age specific probabilities of ovulation were calculated using unweighted means from Smith (1973: Table 2; 1987: Table 11). A random number with a value between 0 and 1 was generated by computer for each animal. This variable was compared to the age specific probability of ovulation based on X_j for each animal. If it was $\leq$ the probability, that animal was considered to be mature. Having fixed the reproductive status of each individual it was then possible to examine the effect of the different assigned ages resulting from the replicate readings. DeMaster's (1978) procedure was used to calculate ASM for each of the eight age distributions (seven readings and their mean). A t'-test (Snedecor and Cochran 1980: 96-98) was used to check for statistical differences between the computed mean ages of sexual maturity.

Simulations were made under three conditions. A random variable was assigned to all animals regardless of sex (756<N<772) for 3 trials. Three trials were also made using the replicate age readings from female seals only

(277<N<287). In another trial only females with data on reproductive status collected in the field (71<N<78) were used. Trials made under the first condition assume no sexual differences in precision of age determination.

Effect of age determination imprecision on growth curves was also investigated. Measurements of body lengths were available for the 1984 and 1986 Resolute seals. For each cross section replicate, mean nose-tail length (NTL) for each age-class was calculated. A logistic curve was fit by graphical methods (Ricklefs 1967), a Gompertz curve was fit by linear regression (Kaufmann 1981), and a von Bertalanffy equation was fit using Proc NLIN of PC/SAS Version 6.03 (Statistical Analysis System for Personal Computers) (Hammill 1987; Smith 1987). Predicted lengths were compared between readings for the equations and between the equations using

$$E = |(P_{at}-P_{bt})/P_{bt}|(100\%)/N$$

as a measure (Roff 1980). P_{at} and P_{bt} are the predicted NTL for a particular reading or a particular growth curve-reading combination, depending on which was being examined. age-class is denoted by t.

Statistical calculations used procedures and custom written programs in PC/SAS Vers. 6.02 and 6.03 run on IBM PCs, ATs, or IBM AT compatible personal computers.

RESULTS

Measures of precision (Tables 2-4) reported here are inversely related to consistency, that is a lower value of the measure indicates greater repeatability between readings.

The side of origin was known for canines from 30 Resolute seals. Both teeth from these animals were cut and differences in precision between left and right side was examined. There was no significant difference (Friedman test $T_2=2.0$ df=1, 29 $0.10<P<0.25$).

No difference was found in the consistency of readings between sexes for Holman cross sections, when mean index of precision (D) was compared by mean age-class ($T_2=0.05$ df=1, 20 $P>0.25$).

The effect of experience can be seen in the measures of precision for the Holman cross sections (Table 2). These data are presented in the order in which they were read and there was an increase in precision with more experience.

Statistical comparisons cannot be made for differences between areas because there is no way to pair teeth from the different areas. For cross sections, readings of Holman teeth appear to be least precise and readings from Svalbard teeth most precise (Table 2). The

1986 Resolute cross sections were read after a period during which no teeth were examined and may reflect lower repeatability as a result. Readings of cementum in toluidine blue stained longitudinal sections were less precise for Holman than for Resolute teeth (Table 3).

Overall, readings of cementum and dentine in stained histological sections of Holman teeth (Table 3) appeared to be less precise than readings of unstained cross sections (Table 2). Conversely cementum and dentine of Resolute teeth stained with toluidine blue (Table 3) had higher precision than cross sections (Table 2). However when readings of teeth from the same individual could be compared there was no significant difference between cross and longitudinal sections for either haemaleum stain (Holman T_2=0.6 df=2, 216 $0.50<P<0.75$) or toluidine blue (Holman T_2=2.9 df=1, 42 $0.05<P<0.10$; Resolute T_2=0.07 df=2, 54 $P>0.75$). The Holman teeth were separated into mean ages calculated from the 21 readings from the 3 treatments. There were no significant differences between the Ds for any of the age-classes with a sample size large enough to allow comparisons to be made. In each case $P>0.25$. Nor was there a difference in precision within sexes, associated with the three treatments (females T_2=0.3 df=2, 94 $P>0.25$; males T_2=0.6 df=2, 120 $P>0.25$) for Holman teeth.

Results were equivocal for within stain comparisons of cementum vs. dentine in haemaleum stained teeth from Holman (Table 3). Similarly differences between cementum and dentine of toluidine blue stained Resolute teeth were small (Table 3).

Comparison of age determinations between Readers 1 and 2 (Table 4) showed them to be statistically different (T_2=19.9 df=1, 41 P<<0.01). The indices of precision for Resolute teeth contain an unequal number of replicates. When D from Reader 1's first 3 readings of 1984 Resolute teeth was compared to D from Reader 3's set of experienced readings, there was a significant difference (T_2=8.5 df=1, 47 P<0.01). In both comparisons the more experienced reader was more consistent in assigning age (Table 4).

Effect of imprecision on population parameters

One-way ANOVA showed there were significant differences in individual age determinations (X_{ij}) among replicates for Reader 1's readings of Holman cross sections (F=2.40 P=0.03) and among his replicates of the dentine in haemaleum stained sections (F=2.57 P=0.02). In both cases Duncan's multiple range test and the least significance difference (LSD) test showed overlap between replicates which did not allow for any generalizations (i.e. age determinations for later readings did not agree more consistently than earlier replicates). Readings of cementum in Holman haemaleum stained sections showed no difference among X_{ij} (F=0.25 P=0.96).

There was a significant difference (Friedman test: T_2=25.9 df=6, 4,338 P<<0.001) in X_i calculated from each of my readings of the Holman cross sections (Table 5). Cross sections of Resolute (1984) teeth (Table 6) likewise had a significant difference (T_2=8.2 df=6, 294 P<0.001) in X_i among readings. X_is from readings of 1986 Resolute cross sections (Table 6) were not significantly different (T_2=2.0 df=6, 456 0.05<P<0.10). Both 1986 (T_2=2.4 df=6, 340) and 1987 (T_2=2.5 df=6, 162) Svalbard teeth (Table 6) had significant differences (0.025<P<0.05) in X_i among readings.

Multiple comparisons of X_i among readings were made. The Holman sample was stored in boxes with N $\approx$ 70, which approximated the total sample size for the Resolute and Svalbard readings. I checked the individual Holman boxes for differences in X_i and did multiple comparisons. These, along with the multiple comparisons from the 1984 Resolute and the Svalbard readings (Figure 3) showed no predictable pattern in placement of a replicate in the multiple comparisons.

For Holman teeth stained with haemaleum (Table 5), both dentine (T_2=12.4 df=6, 900) and cementum (T_2=11.6 df=6, 882) showed highly significant differences ($P<<0.001$) in X_1 between readings. However there was considerable overlap between the readings (Figure 4). A significant difference occurred among the readings of cementum in Holman teeth stained with toluidine blue (Table 5; T_2=2.8 df=6, 306 $P<0.025$), but the overlap between readings was even more extensive (Figure 4).

Resolute sections stained with toluidine blue (Table 7) gave similar results. For cementum on these slides difference in X_1 between readings was significant (T_2=2.5 df=6, 216 $P<0.05$) but separation was extensive (Figure 4). Difference between X_1 from readings of dentine was highly significant (T_2=7.1 df=6, 318 $P<0.001$) and the first reading was separate from the others (Figure 4).

Reader 2 showed a significant difference (T_2=5.2 df=6, 156 $0.001<P<0.005$) in X_1 between readings of cross sections (Table 8). His first reading was higher than his other readings (Figure 5). Reader 3 (Table 8) also had significant differences (T_2=6.4 df=2, 100 $0.001<P<0.005$) but his first reading was the lowest (Figure 5).

Age frequency distributions are used to create life tables and generate stable age distributions. There can be considerable variation in the size of age-classes between replicate readings of cross sections (Figure 6). Frequencies between the readings were not statistically different (chi-square=125.64 df=132 P=0.642). Some variation is retained after smoothing although there is increasing congruence in the numbers calculated for older age-classes. Difference in the stable age distributions derived from the various readings (Figure 7) is slight. The mean maximum difference for the projected age distributions was 0.45% (median=0.265%, range=0.10 to 1.64%). The largest maximum difference occurred in age 1 from the first and third readings. Divergence between readings decreased rapidly to a minimum in ages 6 and 8 and then increased slightly with increasing age.

There was significant difference (chi-square=148.1 df=20 P<0.001) in the read age distributions from Readers 1 and 2 (Figure 8). Only teeth which had been read by both investigators were included. Read distributions were truncated at age 20. Because of differences in the assigned age-classes Reader 1's sample size was 673 while Reader 2 assigned 668 animals to the age-classes 0 to 20 inclusive. However the stable age distributions calculated after these distributions were smoothed differ minimally (Figure 9).

Effect of imprecision on mean age of sexual maturity

When all the specimens were assigned random variables to determine their reproductive status, the smallest difference in mean age of sexual maturity (ASM) was 0.01 years (NS $0.10<P<0.20$) in two of the trials. A difference of 0.03 years occurred 3 times in two trials and was highly significant ($P<0.001$). Significance ($P<0.001$) was assigned to a difference of 0.04 years in one trial. The second smallest difference in one trial was 0.09 years which was highly significant ($P\ll0.001$). It was assumed that once significance had been established for two differences within a trial, larger differences within the same trial would also be statistically different.

Three trials were run, assigning random variates to all the females. In each, the smallest difference in ASM was 0.01 years (NS $P>0.50$). A difference of 0.04 years was significant ($0.01<P<0.025$). Two simulations had a 0.07 year difference which was highly significant ($0.001<p<0.005$) as were three differences of 0.08 years ($p<0.001$).

For females whose reproductive condition was known from the field collections 2 differences in ASM of 0.05 years were not significant ($P>0.50$) nor were two ages of sexual maturity 0.15 years apart ($0.10<P<0.20$). One difference of 0.20 years was significant ($0.01<P<0.025$) while a similar difference between two readings was highly significant ($0.001<P<0.005$) because of disparity in variance. Again larger differences were assumed to be significant.

There were 28 possible comparisons between the calculated ASM for each trial. With such a large number of tests, level of significance can be questionable (Rice 1989). A sequential Bonferroni test (Rice 1989) returns a value of 0.05/28 = 0.0018 for judging the significance of the smallest probability. Since the t'-test gives probabilities which reach levels < 0.001, I am justified in saying the majority of comparisons give statistically significant results.

Effect of imprecision on growth curves

Comparison of predicted nose-tail length (NTL) among replicates for von Bertalanffy and Gompertz curves (Table 9) all had a mean absolute percentage difference (E) < 2% (Tables 10, 11). The greatest difference in a predicted NTL for a specific age was 6.5% for the von Bertalanffy equation and 3.1% for the Gompertz equation. The logistic equation (Table 9) was more variable in predicting NTL but there was only one E > 3% (Table 12). However the greatest percent difference for an age was 13.7.

Kaufmann's (1981) method of calculating a Gompertz curve by fitting a linear regression is advantageous because it allows statistical comparison between the coefficients. I used a *t*-test to check between the most disparate values for slope and intercept which both occurred between replicates 4 and 6. Neither slope nor intercept was significantly different ($P>0.50$). Other slopes and intercepts were not tested, because they were intermediate between the values that were tested and so were unlikely to be statistically different. This result suggests E is useful as an indication of similarity between growth curves.

I also used E to compare between growth curves for each reading (Figure 10). von Bertalanffy and logistic growth curves were the most similar with measures ranging from 0.63 to 2.23%. For individual ages, minimum difference in predicted NTL was 0.008% and maximum difference was 10.88%. Only two of 160 comparisons were 5% and the majority of the remainder were ≤ 3%. von Bertalanffy and Gompertz curves differed by 2.60 to 3.73% with a minimum of 0.03% difference in predicted NTL and a maximum of 7.51% difference for any individual age. The majority of individual comparisons were ≤ 5% different. Gompertz and logistic curves were the most disparate with a range of 2.75 to 5.41%. For individual comparisons the minimum difference in predicted NTL was 0.02% and the maximum was 11.33%. Many individual differences were > 5% and these tended to occur in the 4 to 9 year age-classes.

Although the mean difference between the growth curves is less than 6%, the logistic and von Bertalanffy curves give better empirical fits to these data than does the Gompertz curve (Figure 11). This figure is representative of the results from the other 6 sets of growth curves.

DISCUSSION

Ideally replicates should be made across a series of samples that vary only in a single property (Mandel 1964). In this case it would mean the tooth sections varied only in the number of GLGs. However other properties of the sections, e.g. area of tooth the section was cut from, section thickness, etc., also varied between animals. Further, my analysis violates the assumptions for repeated tests (Hamaker 1986). These assumptions are: (1) results are in statistical control, i.e. the test method can be repeated indefinitely without change and; (2) results are mutually independent, i.e. the outcome of any 1 of the series of tests is not in any way influenced by the other tests in the same series. A person's count is influenced, consciously and unconsciously, by previously read teeth. These problems are unavoidable and are recognized as potential confounding factors.

Violating these assumptions probably underestimates the variance of age determination. While reading the same batch of teeth repeatedly a worker probably notices the same cues. Thus results are more repetitive than if they were all from different teeth. Although each reading was meant to be independent of the others, this was not possible. In certain cases a specific feature e.g. shape of the tooth, made the count memorable. In other cases there is probably a subconscious recognition of some teeth that lowers the variance. Reader 2 did his last six readings on consecutive days (the last two were made on the morning and afternoon of the same day) and this short length of time may have increased his repeatability. For all these reasons variance for one tooth read X times is almost certainly less than variance for X teeth, of the same age, each read once

Equal repeatability was found between sexes and between left and right canines of the same animal. Thus comparisons may be made without regard to sex or side.

Patterns of enamel loops in the third upper molar of muskrats (*Ondatra zibethicus*) were symmetric between sides (Pankakoski and Nurmi 1986). This suggests both sides are affected equally during tooth development.

There do not appear to be age specific differences in levels of precision between cross and longitudinal sections. This conclusion is weak because of the small sample size (2 or 3 animals) in the older age-classes (ages 6, 9, 10, 12). Other age-classes had only 1 animal and therefore could not be tested.

Evidence for geographic differences in repeatability of age estimates is circumstantial. Cause of IGL formation is uncertain. If calcification processes are related to food, either through levels of available energy, nutrients, or minerals, geographical differences in precision of age determination might result from differences in quantity or quality of food between regions (Lowry et al. 1980). Harbour seals (*Phoca vitulina*) have a fairly constant diet within and between years, but there are diet differences between areas (Härkönen 1987). Geographical variation because of distribution of prey and seasonal differences because of movements of prey and seals have been shown for the Weddell seal (*Leptonychotes weddellii*: Green and Burton 1987). Such changes might affect the developing tooth structures.

Geographic differences in body size of ringed seals (e.g. Hammill 1987; Lydersen and Gjertz 1987) have been noted and suggest distinct populations. On the other hand, returns from tagging experiments show seals can move considerable distances (Smith 1987: Table 4). The effect on geographic differences would depend on how much movement there was, whether the movement was migration or dispersal, and the fate of seals that moved versus the fate of sedentary seals. Fedoseev (1975) and Finley et al. (1983) suggest there are ecotypes of ringed seals which depend more heavily on habitat differences than on geographic isolation.

That an inexperienced reader had greater precision reading the Resolute teeth, than an inexperienced albeit different reader had reading the Holman teeth (compare Reader 3-Naive from Table 4 to boxes 81-805 and -728 from Table 2) suggests there are population differences in distinctiveness of layering. Ian McLaren (Dep't. of Biology, Dalhousie University, Halifax, N.S. B3H 4J1, in litt.) commented he remembered eastern Arctic teeth to be more distinct than Holman teeth he examined. Helle (1980) looking at seal teeth from Bothnian Bay and without direct reference to other areas says "layered structure,...is highly distinctive" (p. 16). It is not clear whether he is referring to stained or unstained sections.

There appears to be geographic differences in readability of harbour seal teeth (compare Fisher 1954 to Bishop 1967). There are indications of regional differences in repeatability or clarity of tooth sections in other mammals (van Nostrand and Stephenson 1964; Roberts 1978; Marsh 1980a). Such differences might be related to storage time or conditions which are seldom documented.

Apparent geographical difference in reproducibility of age readings reported here was confounded by differences in "newness" of the specimens. Storage time of cross sections from Holman was greatest, while that for Svalbard teeth was least. The effect of length of storage and storage conditions on precision of age determinations needs to be examined.

Cross sections of canines were originally chosen because of the ease with which they could be processed (Tikhomirov and Klevezal 1964; Smith 1973). Many workers favour stained longitudinal sections (e.g. Stirling et al. 1977; Helle 1979), however this cannot be justified based on results of precision given here. Moreover, preparation of cross sections is faster than preparation of histological sections and therefore makes more sense economically for large collections. Cementum was more easily and quickly read than dentine in stained sections.

No difference could be detected between repeatability for either of the two stains used. Thomas (1977) suggested toluidine blue made teeth of various species of terrestrial mammals easier to read. This is a subjective assessment of course, but it also seems to hold for the ringed seal. Permanent mounts of sections faded quickly if 0.032% toluidine blue was used. Subsequent work indicated 2% toluidine blue is useful for permanent mounts. Good results have been obtained using a variety of other stains (Stone et al. 1975). Further work on different stains and the associated precision of age determination is justified.

Not surprisingly there was a difference between readers. Just as Miller (1974) points out there is an "ability factor" which enables some workers to evaluate material more accurately than others, there is an ability factor which enables some workers to evaluate material more precisely than others. This is probably innate to some degree but is also likely developed with experience (Stirling 1969; Williams and Bedford 1974). Formation of a relatively "clear," fixed image of the IGLs in the reader's mind probably correlates with level of experience.

Stenson and Myers (1988) found experienced observers without current practice and inexperienced observers had similar variability in classifying hooded seal (<u>Cystophora cristata</u>) pups into 3 age stages. This illustrates repeated periods of practice will aid retention of a prototype in memory (Wickelgren 1981). It is likely an experienced reader would take a shorter time to regain a level of consistency than it would take a naive reader to reach that same level. Establishment of sets of learning cross sections and slides would facilitate reacquaintance with decision criteria. Ideally these would be from known age animals.

The apparent age distribution affects the value of the measures of precision. Because the measures are ratios, an absolute deviation in a younger age-class will result in a larger value than it would in an older age-class. Comparison between observers is thus made difficult as one reader may perceive a younger age distribution. This will tend to result in higher values of the measures of precision giving the appearance of lower precision. For example, Reader 3 (Table 4) appears to be less precise with more experience. This can be explained, at least in part, by the lower mean ages of the experienced readings (Table 8). Differences between Readers 1 and 2 can likewise be attributed in part to differences in mean ages between their readings (Table 8).

What makes ringed seal teeth so difficult to read? In unstained dentinal cross sections it is lack of clarity and contrast between opaque and translucent IGLs. This lack of contrast forces a reader to make many subjective decisions during a session which may be made differently at another time. In comparison, harp seal (Phoca groenlandica) teeth have distinct IGLs (Bowen et al. 1983: Figure 3) and are much easier to read (pers. obs.).

No known age animals were available to learn what an IGL looks like. It is thus up to each reader to formulate his own decision rules. These change with experience and over time. Similarly, lack of known age animals does not allow criteria to be developed for judging the appearance of an adventious line. What was considered an adventious line once might be considered a true growth layer at another time.

Unlike tree rings, fish scales or otoliths, where growth rings accumulate on the outside of the structure, dentine fills inward--into an ever decreasing space. GLGs deposited at an older age are narrower than early GLGs and decisions must be made whether to count narrow inner lines as IGLs or to dismiss them as adventious. To compound the problem, narrow GLGs often cannot be followed completely around the pulp cavity. This problem of narrow inner layers is not unique to ringed seals of course, but with the pulp cavity staying open for a long time in pinnipeds generally, more narrow GLGs accumulate than in terrestrial mammals.

Although a decline in width of GLGs occurs as animals age (pers. obs.; Smith 1973: Figure 5), width of IGLs is not a reliable criterion for making decisions. Stewart and Stewart (1987) found inter-year differences in dentine thickness and diameter of maxillary canines of harp seal neonates. Similarly, amount of dentinal material deposited during any year in the canines of older, known age harp seals may be greater or smaller than the amount in preceding years (Bowen et al. 1983: Figure 5). Such variation would also be expected in ringed seals. Indeed, Smith (1973) shows considerable overlap in the 95% confidence intervals of measurements of dentinal GLGs between ages. Asymmetric growth in the width of dentine has been noted in harp seal canines (Bowen et al. 1983). Therefore results would be affected by the side on which measurements were made. It is often impossible to distinguish the sides of the tooth so measurements could not consistently be taken on the same side.

There are technical problems in assessing the expected width of GLGs. Measurements using an eyepiece micrometer would be affected by the angle at which the eye was held to the micrometer. Differences in location at which sections were cut would affect the width of GLGs. Finally if cross sections were not perfectly perpendicular to the IGLs, but were somewhat oblique, there would be an error (Klevezal 1964). Biological variation and technical considerations make measurements of GLG width unreliable criterion for increasing precision of age determination.

For routine reading, increase in magnification did not increase resolution between IGLs and in some cases, actually decreased resolution. Additional magnification often seemed to increase overall opacity of the specimen. Intensifying the transmitted light often did not compensate for the heightened opacity. In a few ringed seal teeth some IGLs change opacity around their circumference. Similarly, changing orientation of the section relative to the reflecting mirror or changing the angle of the mirror may make differences between IGLs more obvious, but it was also observed to reverse opacity of IGLs in some sections. These phenomena have also been reported in harbour (Bishop 1967) and southern elephant seals (Mirounga leonina; Carrick and Ingham 1962). Peabody (1961) points out each fossil bone section used for age determination presents a unique problem of lighting. The same situation applies to ringed seal teeth. Differences in setting of the mirror will affect the perception of sections even if the reader has an image of IGLs (width, etc.) firmly fixed in his mind. Changes in opacity resulting from differences in orientation of sections to the light would render attempts at machine reading imprecise as well.

Opacity of cemental growth layers in stained longitudinal sections was not noticeably affected by changes in intensity or angle of illumination. Cemental IGLs seem to grow at a more constant rate than dentinal IGLs. Nonetheless there were problems with stained sections which made them difficult to read consistently. Variability in staining relates to individual sections, at least in part. Sections from the same tooth, on the same slide, and coloured with the same dye vary in readability. Even within one section the definition and degree of staining of successive lines may be irregular. This has also been commented on for other species such as the African buffalo (Syncerus caffer; Grimsdell 1973). Variability between sections makes it difficult to form an image of the appearance of IGLs in the cementum. It may happen a worker will have a run of well stained teeth and then read a poorly stained slide. Such a situation may make it more difficult to interpret the poorly stained section because the reader has become habituated to well stained slides.

Selection of site at which to read the cemental GLGs can also affect repeatability. Layers along the lateral sides of the tooth are parallel but closely spaced. Near the apex of the tooth they spread out but they also tend to become wavy with irregular spacing between the layers. Also in this area the narrow dark stained layers tend to fuse and diverge. Similar descriptions of cementum have been published for a variety of species (e.g. Grimsdell 1973; Heggberget 1984; Mason 1984; Jean et al. 1986 and many others). The reader is faced with the dilemma of reading the cementum along the tooth where the layers are generally straight but close together and difficult to discriminate or at the end of the root where the layers are more widely separated but ramifications of cemental lines occur to confuse the count. Choosing either area means the worker has to make subjective judgments which will lead to variability between counts. Reproducibility between teeth will also be affected by how standardized the site of counting can be. Since the area of choice, whether it be along the side or near the root, is not always available (e.g. sections may be curled or part of the section may be missing) repeatability will suffer.

Generally the thickest and most readable dentine is on the dorsal side of the tooth. There is no easy, objective way to assess dentine thickness because of the way the thickness changes along the root.

Population parameters

Statistically significant differences were found in mean ages (X_i) from the replicate readings of the same teeth. This was up to 0.7 years for cross sections. DeMaster (1981) suggested it may be possible to use changes in the mean age of populations as they grow to determine which age-classes density dependent mechanisms were operating on. However my work shows variance in age determination can affect comparisons of mean ages.

Lydersen and Gjertz (1987) compared their mean age to that of Helle (1979). However Helle (1979) clearly stated he did not consider his age structure representative of the population. Furthermore Lydersen and Gjertz (1987) collected in the spring on ice while Helle (1979) netted his animals in the fall. Comparisons of mean age between populations will be confounded by variance in the readings, time and method of collection, and conditions during collection (e.g. presence or absence of ice). The first factor probably has the least effect on such comparisons.

My first reading has a tendency to give a mean age lower than the other readings. Multiple comparison shows overlap with at least one other reading in 5 of the 6 occurrences when the first reading appeared in the lowest or second lowest ranking, so it is difficult to generalize about the position of any of the readings. However it suggests that if teeth are read only once they will tend to give a younger age distribution than if they are examined a number of times. In contrast Reader 2's first examination of the cross sections was statistically higher than his other readings, which were indistinguishable. These results suggest repeated examination of the same tooth may change the assigned age considerably.

For a number of reasons life tables and Leslie matrices are not appropriate techniques for investigating population growth of ringed seals. Use of these techniques from a single age distribution is valid only if the population is stable (Van Sickle 1988). Smith (1987) shows there are year-to-year variations in q_x (mortality) and m_x (fecundity) rates for ringed seals. Furthermore there is the difficulty of calculating the correct values of P_x (survival) and F_x (fecundity) for use in the Leslie matrix (Caughley 1977). I used the values directly from the life table, although these are not strictly correct, to investigate the effect variance in age determination had on population projections. It is clear this approach is insensitive to differences in the read age distributions. It is not surprising frequencies which are not statistically different (Figure 6) gave similar stable age distributions (Figure 7). However even age distributions that are significantly different (Figure 8) gave very similar stable age distributions (Figure 9). This is largely attributable to the smoothing necessary for these calculations.

It can be questioned whether taking the mean of the seven readings is an acceptable practice. In some cases the mean is a value that was never assigned to the tooth. To examine this, I calculated the stable age distributions from both the mean and the median. The difference between these two measures of central tendency is small (Figure 12) and insignificant to management recommendations.

One population parameter where there was differences between the readings and between readers is the estimate of lambda (finite rate of increase). The estimate varied above or below 1 between readings and between readers of the same teeth. With the circularity involved in calculation of lambda from a single age distribution (Van Sickle 1988), the validity of any of the calculated values is questionable.

Average age of sexual maturity

In my simulations reproductive status was kept constant but the age-class a particular seal was assigned to, varied between readings. This changed the distribution of mature versus immature animals and gave statistically different age of sexual maturity (ASM) among the replicate readings.

DeMaster (1978) calculated a sample size of ≈ 25 in each of the indeterminate age-classes is necessary to detect differences ≥ 0.5 years. With sample size ≈ 765, when using all the animals, N in the indeterminate age-classes (i.e. ages 3 to 9) was commonly 2 to 3 times this size. These large sample sizes result in small variance and made detection of small differences in ASM (i.e. 0.03 years) possible. When I used only the females (N ≈ 250) the number in each of the indeterminate age-classes approximated 25 and differences of the same magnitude were significant. When I examined only the females with known reproductive status ($N \approx 75$), sample size in each of the indeterminate classes was < 10. Yet even here a difference of 0.20 was judged significant.

Upon elimination of teeth with missing values in any of the replicate readings, ASM changed slightly. However conclusions drawn about differences between readings were not qualitatively affected. The majority of readings still appeared to come from distinct populations.

Comparing ASM for any of the readings to published data (Smith 1987) or other data from which I could calculate ASM (Smith 1973: Table 8; Hammill 1987: 93) suggested the populations had different ages of sexual maturity. However the difference between the results for the various readings from a particular trial and one of the populations from the literature varied from 0.04 to 2.74 years. While differences in age determination may not affect our judgment as to whether two populations have a different ASM, they certainly affect the apparent magnitude of the differences.

If these results had come from populations collected at different times or in different places, few biologists could refrain from publishing such apparently significant results. This work should serve as a caution against uncritical acceptance of ASM derived from statistical tests which do not incorporate measures of the precision of age determination. Validity of any particular ASM may be questionable because of differences in age readings. Examination of population trends through changes in ASM (e.g. Bengtson and Laws 1985) would be difficult for ringed seals because variability in age determinations from teeth is great enough to create spurious differences in ASM. Confidence in accepting differences in ASM would be greater if the ages were based on an independent method of assessing age, e.g. tags.

Growth curves

Other workers have found sexual dimorphism in growth curves of ringed seals (McLaren 1958; Hammill 1987; Lydersen and Gjertz 1987; Smith 1987). I pooled data from both sexes for two reasons. I wanted a sample size large enough that the results were caused by differences in readings and were not a result of random events caused by small sample size. Secondly, I am not claiming any of my curves represent growth in ringed seals, so the predicted lengths are not that important. The question I wish to address is how variation between age readings affects the growth curves.

My results indicate variation in age determination has little effect on predicted lengths from logistic, Gompertz, or von Bertalanffy equations. The logistic equation was more variable than the other two equations, but this may be a result of the technique used to fit the logistic curve. Nonetheless the technique gave a reasonable fit to the data and relatively good comparison to the other fitted growth curves.

There are several difficulties in fitting growth curves to a shot sample of wild animals. First the data is neither cross-sectional nor longitudinal. Each measurement comes from an individual which is assumed to have grown at the same rate at previous ages as the present representatives of that age-class i.e. growth is assumed age-specific and independent of year. Temporal environmental changes would be expected to affect the growth trajectory. Secondly the length of time between measurements of animals in adjacent age-classes is not constant i.e. animals classified as 3 year olds are not exactly one year older than animals classified as 2 year olds, so the calculated growth rate is not strictly accurate. Finally because the animals are not of known age, they may or may not be assigned to the correct age-group.

Growth curves and their accompanying estimates of asymptotic length are important for detecting changes in maturation rates and age and relating these to changes in density, abundance of food, etc. (Sergeant 1973). Furthermore, growth curves can be used to estimate the population's energy requirements as a step in determining its effect on prey species (Harwood and Croxall 1988). Monitoring populations would be difficult because growth curves are relatively insensitive to changes in populations.

Precision of determining age in ringed seals appears to less than in other species (Table 13). This amount of imprecision can have an effect on some of the parameters commonly used to assess the state ot populations. The amount of precision which is necessary to allow valid statements to be made about differences within a population over time or between populations must be theoretically determined. In the meantime, workers should routinely report the level of precision in age estimates.

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Table 1 Details of decalcified, longitudinal, stained sections. Dentine of Holman teeth stained with toluidine blue was judged unreadable.

Location (Year)	Type of stain	Structure read	# of slides	# of animals
Holman	Haemaleum	Cementum	150	139
		Dentine	163	151
	Toluidine blue	Cementum	55	49
Resolute (1984)	Toluidine blue	Cementum	37	37
		Dentine	56	56

Table 2 Measures of precision for cross sections of ringed seal teeth. Data is presented in the order in which the boxes of teeth were read. Boxes with single spacing between them were read concurrently.

Box	N	Index of average error	Average V	Average D
Holman				
81-805	68	0.3340	0.4296	0.1641
81-728	74	0.2519	0.3338	0.1262
81-95	65	0.1985	0.2624	0.0997
81-179	52	0.1827	0.2376	0.0889
81-256	75	0.1758	0.2295	0.0868
81-333	58	0.1731	0.2229	0.0846
81-410	39	0.1735	0.2309	0.0876
81-487	42	0.2055	0.2660	0.1013
81-568	74	0.1794	0.2353	0.0897
81-645	74	0.1949	0.2646	0.1008
Various1	71	0.1647	0.2132	0.0810
Various2	75	0.1651	0.2202	0.0832
Combined		0.2008	0.2635	0.1001
Resolute 1984	54	0.1455	0.1918	0.0729
Svalbard				
Assorted	53	0.0384	0.1173	0.0455
PHNA86-1	29	0.1262	0.1684	0.0640
PHNA87	29	0.1180	0.1655	0.0627
Resolute 1986				
Xsections	46	0.2534	0.3438	0.1315
Sides	63	0.1505	0.1920	0.0742

Table 3 Measures of precision for stained longitudinal sections.

	N	Index of average error	Average V	Average D
Holman-Haemaleum stain				
Cementum				
Slide box 1	70	0.1914	0.2585	0.0977
Slide box 2	80	0.3060	0.3704	0.1401
Combined		0.2525	0.3181	0.1205
Dentine				
Slide box 1	70	0.3651	0.4831	0.18[illegible]8
Slide box 2	93	0.2433	0.3190	0.1222
Holman-Toluidine blue stain				
Cementum	55	0.2642	0.3534	0.134[illegible]
Resolute-Toluidine blue stain				
Cementum				
1984	37	0.0815	0.1097	0.0416
Dentine				
1984	56	0.1092	0.1506	0.0572

Table 4 Comparison of precision between readers for cross sections. The measures refer only to sections read by both observers.

	Index of average error	Average V	Average D
Holman (7 readings of 42 teeth)			
Reader 1	0.1832	0.2403	0.0910
Reader 2	0.1290	0.1771	0.0691
Resolute (48 teeth)			
Reader 1 (7 readings)	0.1426	0.1874	0.0711
Reader 3-Naive (3-5 readings)	0.1376	0.1817	0.0914
Reader 3-Experienced (3-4 readings)	0.1643	0.2189	0.1224

Table 5 Number, minimum age, maximum age, and mean age of the frequency distribution (X_1) for the age readings of Holman teeth.

Replicate	N	Min	Max	X_1	Replicate	N	Min	Max	X_1
Cross sections					Dentine -haemaleum stain				
1	756	0	30	5.73	1	159	0	12	3.48
2	764	0	30	6.20	2	161	0	24	3.67
3	767	0	39	6.47	3	160	0	22	3.73
4	765	0	34	6.45	4	162	0	33	4.36
5	765	0	38	6.21	5	159	0	31	4.26
6	762	0	34	6.21	6	162	0	32	4.76
7	768	0	31	5.81	7	163	0	31	4.79
Cementum -haemaleum stain					Cementum -toluidine blue stain				
1	148	0	24	3.81	1	54	0	13	3.56
2	150	0	28	4.11	2	54	0	15	3.63
3	150	0	21	3.59	3	55	0	16	3.89
4	150	0	23	3.80	4	55	0	15	3.55
5	150	1	23	4.03	5	55	0	15	3.96
6	150	0	25	4.01	6	55	0	16	3.76
7	150	0	26	4.03	7	54	0	16	3.78

Table 6 Number, minimum age, maximum age, and mean (X_1) of age determinations for replicate readings of cross sections.

Reading	N	Min	Max	X_1
Resolute				
-1984				
1	53	0	19	5.49
2	51	0	20	5.69
3	53	0	19	5.89
4	54	0	20	6.56
5	53	0	36	6.40
6	54	0	23	6.07
7	54	0	21	6.11
-1986 Xsections				
1	44	0	21	6.09
2	44	0	17	5.25
3	44	0	26	5.73
4	46	0	16	5.91
5	46	0	18	5.91
6	46	0	18	6.28
7	46	0	14	5.85
-1986 Sides				
1	60	0	18	7.62
2	59	0	21	7.47
3	60	0	19	7.05
4	60	0	21	7.22
5	63	0	19	7.57
6	62	0	17	6.90
7	62	0	20	7.97
Norway				
-PHNA86-1				
1	29	0	22	6.34
2	29	0	21	6.00
3	29	1	20	6.03
4	29	1	23	6.21
5	28	1	21	5.71
6	28	1	25	6.04
7	29	1	22	6.28
Assorted 1986				
1	50	1	18	7.54
2	46	1	18	7.63
3	50	1	18	7.68
4	52	1	18	7.73
5	51	1	17	7.59
6	53	1	18	8.00
7	53	1	18	7.92
-1987				
1	29	1	20	4.62
2	29	0	20	4.41
3	29	1	20	4.52
4	28	1	12	3.61
5	29	1	23	4.52
6	29	1	20	4.38
7	29	1	24	4.48

Table 7 Number, minimum age, maximum age, and mean (X_1) of age determinations for replicate readings of Resolute histological sections.

Reading	N	Min	Max	X_1
<u>Toluidine blue stain</u>				
-cementum				
1	37	2	28	59
2	37	0	32	9.73
3	37	2	30	10.11
4	37	2	33	10.57
5	37	2	32	10.08
6	37	2	31	9.73
7	37	2	31	9.73
-dentine				
1	55	0	23	4.84
2	54	0	25	5.59
3	56	0	26	5.80
4	56	0	25	5.95
5	56	0	26	5.68
6	56	0	27	5.79
7	56	0	27	5.88

Table 8 Number, minimum age, maximum age, and mean (X_1) of age determinations for comparison between readers. The data include only teeth read by each observer.

Reading	N	Min	Max	X_1
Holman				
Reader 1				
1	42	1	22	6.81
2	42	1	26	7.29
3	42	1	23	7.12
4	42	1	24	6.31
5	42	1	19	5.88
6	41	1	23	5.37
7	42	1	22	5.43
Reader 2				
1	39	1	34	8.85
2	38	1	27	7.18
3	38	0	28	7.82
4	40	0	28	7.38
5	41	1	21	7.29
6	39	1	27	7.54
7	42	1	26	7.38
Resolute 1984				
Reader 1				
1	48	0	19	5.25
2	46	0	20	5.52
3	47	0	19	5.62
4	48	0	20	6.17
5	47	0	36	6.19
6	48	0	23	5.88
7	48	0	21	5.94
Reader 3-Naive				
1	48	0	35	9.02
2	48	0	32	10.83
3	48	1	34	10.33
4	32	3	36	13.06
5	20	3	33	16.20
Reader 3-Experienced				
1	48	0	22	6.08
2	48	0	24	6.60
3	48	0	26	7.17
4	14	8	26	14.14

Table 9 Logistic, Gompertz and von Bertalanffy growth equations fit to 1984 and 1986 Resolute ringed seal nose-tail lengths (NTL). t is age in years and R^2 is the coefficient of determination from regression.

Logistic

Reading		R^2
1	$NTL=\dfrac{137.95}{1+\exp(-0.322(t+1.324))}$	0.95
2	$NTL=\dfrac{144.45}{1+\exp(-0.202(t+2.469))}$	0.85
3	$NTL=\dfrac{143.39}{1+\exp(-0.188(t+3.641))}$	0.81
4	$NTL=\dfrac{140.50}{1+\exp(-0.208(t+3.070))}$	0.91
5	$NTL=\dfrac{141.50}{1+\exp(-0.334(t+0.436))}$	0.95
6	$NTL=\dfrac{138.70}{1+\exp(-0.382(t+0.562))}$	0.97
7	$NTL=\dfrac{139.75}{1+\exp(-0.327(t+0.791))}$	0.95
mean	$NTL=\dfrac{141.50}{1+\exp(-0.215(t+2.623))}$	0.94

Gompertz

Reading	
1	$NTL=139.46\cdot\exp(-\exp(-0.187(t+3.775)))$
2	$NTL=140.46\cdot\exp(-\exp(-0.177(t+3.654)))$
3	$NTL=143.43\cdot\exp(-\exp(-0.175(t+3.478)))$
4	$NTL=140.85\cdot\exp(-\exp(-0.168(t+3.859)))$
5	$NTL=140.19\cdot\exp(-\exp(-0.176(t+3.584)))$
6	$NTL=140.06\cdot\exp(-\exp(-0.191(t+3.264)))$
7	$NTL=140.26\cdot\exp(-\exp(-0.178(t+3.542)))$
mean	$NTL=141.80\cdot\exp(-\exp(-0.176(t+3.605)))$

von Bertalanffy

Reading	
1	$NTL=136.43(1-e^{(-0.28t-0.86)})$
2	$NTL=139.36(1-e^{(-0.23t-0.86)})$
3	$NTL=138.61(1-e^{(-0.24t-0.88)})$
4	$NTL=137.95(1-e^{(-0.25t-0.78)})$
5	$NTL=139.14(1-e^{(-0.24t-0.81)})$
6	$NTL=137.49(1-e^{(-0.27t-0.82)})$
7	$NTL=138.82(1-e^{(-0.27t-0.75)})$
mean	$NTL=140.94(1-e^{(-0.20t-0.81)})$

Table 10 Comparison of lengths predicted by the Gompertz growth equation for the various replicates. Difference is expressed as mean absolute percentage difference (E).

Replicate (n)	Replicate (n+1) 2	3	4	5	6	7	mean
1	0.81	1.36	1.19	1.18	0.65	1.04	0.87
2		1.40*	0.44+	0.48+	0.50	0.31+	0.70*
3			1.82+	1.86+	0.95+	1.69+	0.70
4				0.18	0.93	0.25	1.14*
5					0.92*	0.17*	1.19*
6						0.74+	0.38
7							1.02*

* Predicted lengths for age n+1 were all smaller than predicted lengths for age n

+ Predicted lengths for age n+1 were all greater than predicted lengths for age n

Table 11 Comparison of lengths predicted by the von Bertalanffy growth equation for various replicates. Difference is expressed as mean absolute percentage difference (E).

Replicate (n)	Replicate (n+1) 2	3	4	5	6	7	mean
1	1.10	0.78	1.28	1.32	0.60	1.44	1.48
2		0.39	0.99	0.27	0.67	0.70	0.51
3			1.05	0.61	0.47	0.86	0.72
4				0.76	0.87	1.10	1.26
5					0.76	0.56	0.73
6						0.86	1.18
7							1.15

Table 12 Comparison of lengths predicted by the logistic growth equation for the various replicates. Difference is expressed as mean absolute percentage difference (E).

Replicate (n)	Replicate (n+1) 2	3	4	5	6	7	mean
1	2.11	1.97	1.66	2.39	1.27	1.29	1.61
2		1.17	1.53	2.26	2.68	1.96	0.89
3			1.35*	2.74	2.63	2.13	1.01*
4				3.43	2.66	1.89	0.65
5					1.57	1.12	2.81
6						0.84	2.39
7							1.85

* Predicted lengths for age n+1 were all smaller than predicted length for age n

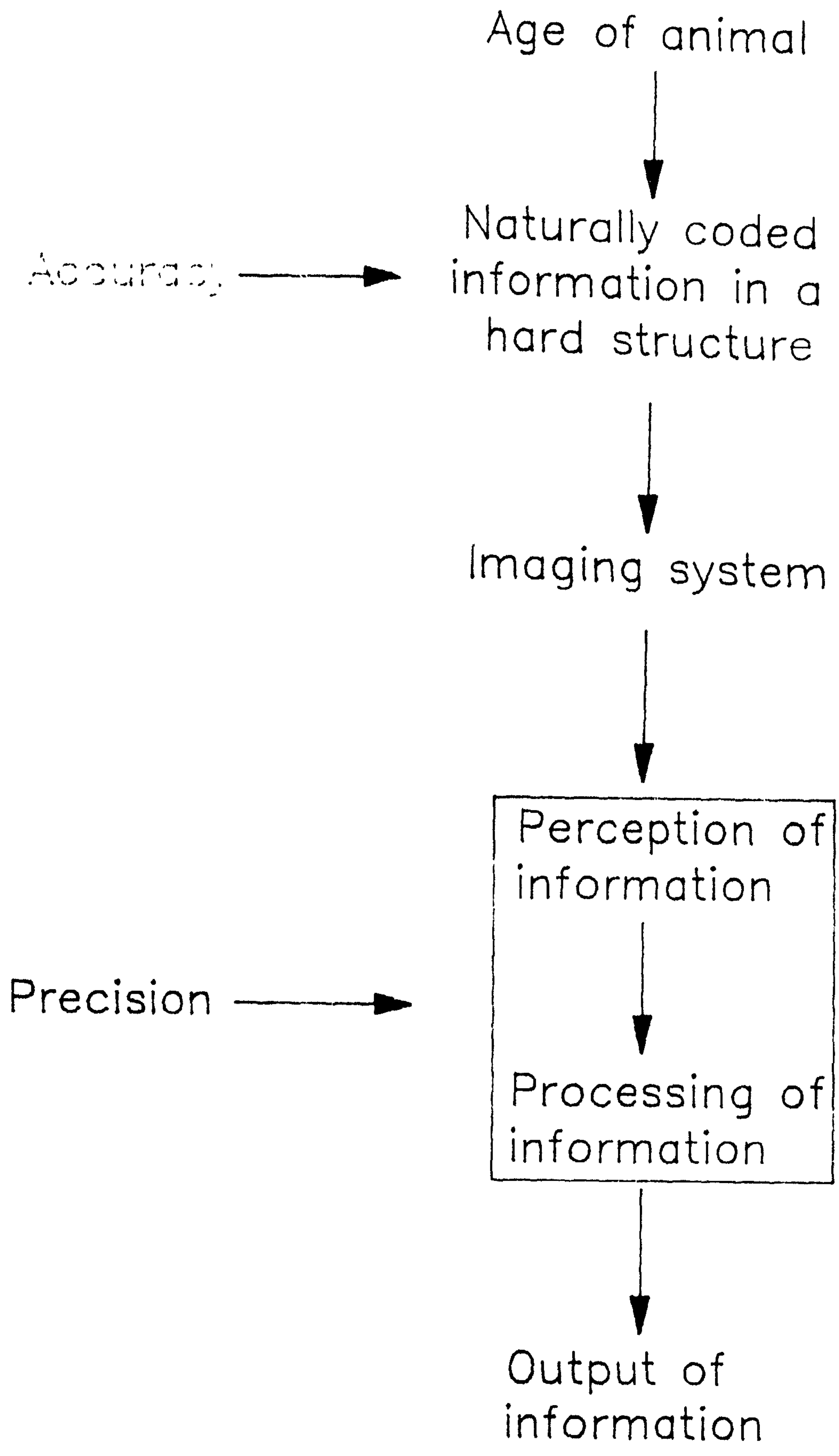
Table 13 Measures of precision (IAE, D, and V) for a variety of species.

Species	# of Observers	# of Replicates	Structure	IAE	D	V
1 Antarctic plunderfish (*Harpagifer bispinis antarcticus*)	2	3	otoliths	0.043-0.255		
2 Arctic grayling (*Thymallus arcticus*)	2		fin rays otoliths scales	0.071 0.098 0.276		
3 Atlantic blue marlin (*Makaira nigricans*)	1 1	3 3	dorsal spine sections	0.020 0.090	0.008 0.084	
4 Atlantic bluefin tuna (*Thunnus thynnus*)	2		whole vertebrae & vertebral sections	0.003-0.063	0.003-0.041	0.004-0.071
5 Arctic fox (*Alopex lagopus*)	1		canine cementum	0.0283-0.2279	0.0104-0.1236	0.0232-0.2932
6 Rough toothed dolphin (*Steno bredanensis*)		3	cementum	0.0991	0.0773	0.1339
7 Narwhal (*Monodon monoceros*)	 3-8 4-5	 1 1	dentine untreated acid etched	 0.2156 0.1369	 0.0711 0.0819	 0.2781 0.1789
8 Cape porcupine (*Hystrix africaeaustralis*)		10	cementum of maxillary teeth			0-1.17 (0.20<V<0.50 for most)

1 Daniels 1983. 2 Sikstrom 1983. 3 McGowan et al. 1987. 4 Prince et al. 1985. 5 Hammill 1983.

6 data from Miyazaki 1980. 7 data from Hay 1984. 8 van Aarde 1985.

Figure 1 The process of age determination from physical features in hard structures of animals. Model is modified from Sych (1974).



Age of animal
Naturally coded information in a hard structure
Accuracy
Imaging system
Perception of information
Precision
Processing of information
Output of information

Figure 2 Ringed seals used in this study came from 3 geographic areas: * Amundsen Gulf (Holman) (1978 n=1; 1979 n=15; 1980 n=7; 1981 n=759); ▲ Barrow Strait (Resolute) (1984 n=61; 1985 n=2; 1986 n=69); ◆ Svalbard (1986 n=77; 1987 n=29).

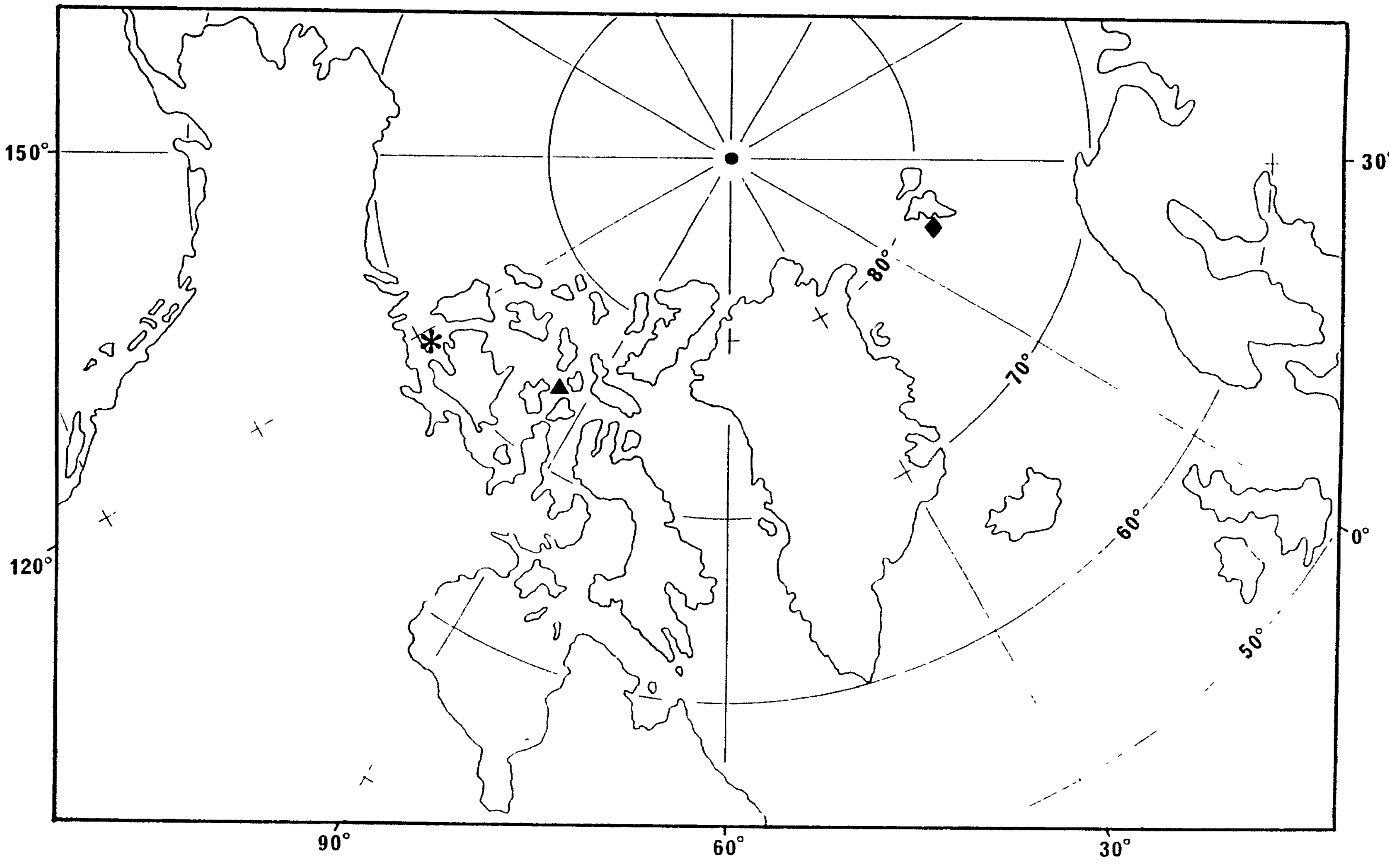

150°
120°
30°
0°
80°
70°
60°
50°
90°
60°
30°

Figure 3 Multiple comparisons of mean age (X_i) between replicates. Replicates with a common underline are not significantly different (α=0.05). R_j is the sum of the ranks from the Friedman test.

Cross sections

Holman								
	Replicate #	1	7	2	6	5	3	4
	R_j	2555.5	2589.0	2861.0	2898.5	3014.0	3174.5	3179.5

Resolute (1984)								
	Replicate #	1	2	7	6	3	5	
	R_j	144.0	178.5	197.0	202.0	208.5	224.0	246.0

Svalbard (1986)								
	Replicate #	5	2	1	3	4	6	7
	R_j	237.5	241.0	261.5	262.5	264.0	285.0	296.5

Svalbard (1987)								
	Replicate #	4	7	5	6	3	2	1
	R_j	92.5	104.0	107.5	109.5	116.5	122.5	131.5

Figure 4 Multiple comparisons of mean age (X_i) between replicates. Replicates with a common underline are not significantly different (α=0.05). R_j is the sum of the ranks from the Friedman test.

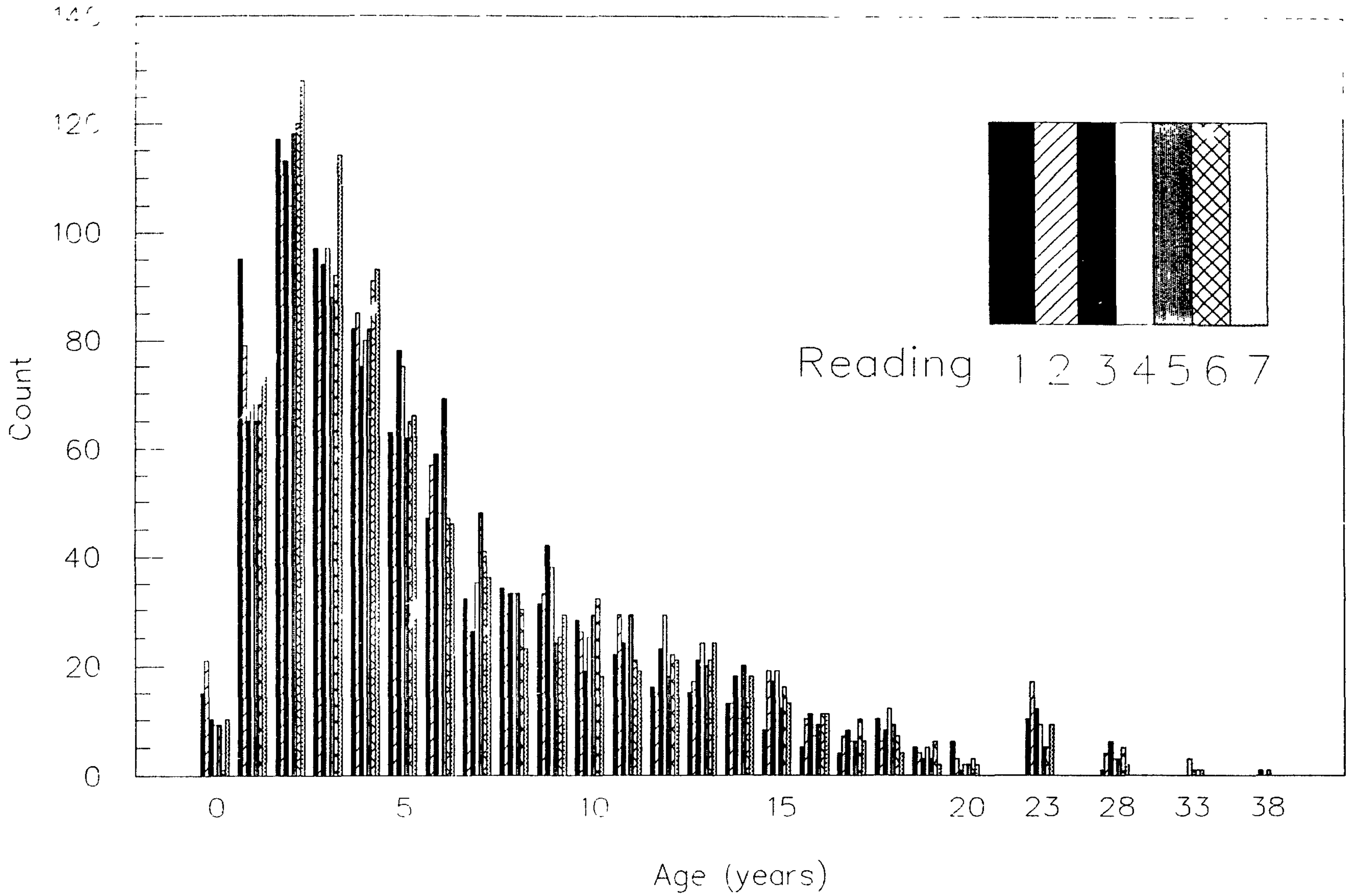
Stained sections

Holman Cementum Haemaleum	Replicate #	1	3	4	2	7	6	5
	R_j	494.0	506.0	583.5	616.5	633.5	646.0	662.5
		———	———		———	———	———	———
				———	———	———		
Holman Dentine Haemaleum	Replicate #	3	1	2	5	4	7	6
	R_j	525.0	529.5	534.5	627.5	638.0	685.0	688.5
		———	———	———	———	———	———	———
Holman Cementum Toluidine blue	Replicate #	1	4	2	5	6	3	7
	R_j	181.5	192.0	203.0	217.0	217.0	217.5	228.0
		———	———	———				
			———	———	———	———	———	
				———	———	———	———	———
Resolute Cementum Toluidine blue	Replicate #	7	6	1	2	5	3	4
	R_j	132.5	134.0	138.5	143.0	151.5	155.0	181.5
		———	———	———	———	———	———	
							———	———
Resolute Dentine Toluidine blue	Replicate #	1	5	6	7	3	2	4
	R_j	155.0	214.5	220.0	224.5	226.5	230.0	241.5
			———	———	———	———	———	———

Figure 5 Multiple comparisons of mean age ($\bar{X}_i$) between replicates. Replicates with a common underline are not significantly different (α=0.05). R_j is the sum of the ranks from the Friedman test.

Reader 2 (Holman cross sections)	Replicate #	2	4	6	5	7	3	1
	R_j	93.5	94.5	95.0	100.5	102.0	119.0	151.5
Reader 3 (Resolute cross sections)	Replicate #			1	2	3		
	R_j			88.5	103.0	114.5		

Figure 6 Frequency distribution of the age classes for the seven replicate readings of Holman cross sections. Age classes > 20 years were pooled and are designated by the median value.



Reading 1 2 3 4 5 6 7
Count
0
20
40
60
80
100
0
5
10
15
20
23
28
33
38
Age (years)

Figure 7 Stable age distributions from the various replicates. For clarity only the stable age distributions for the odd numbered replicates are shown.

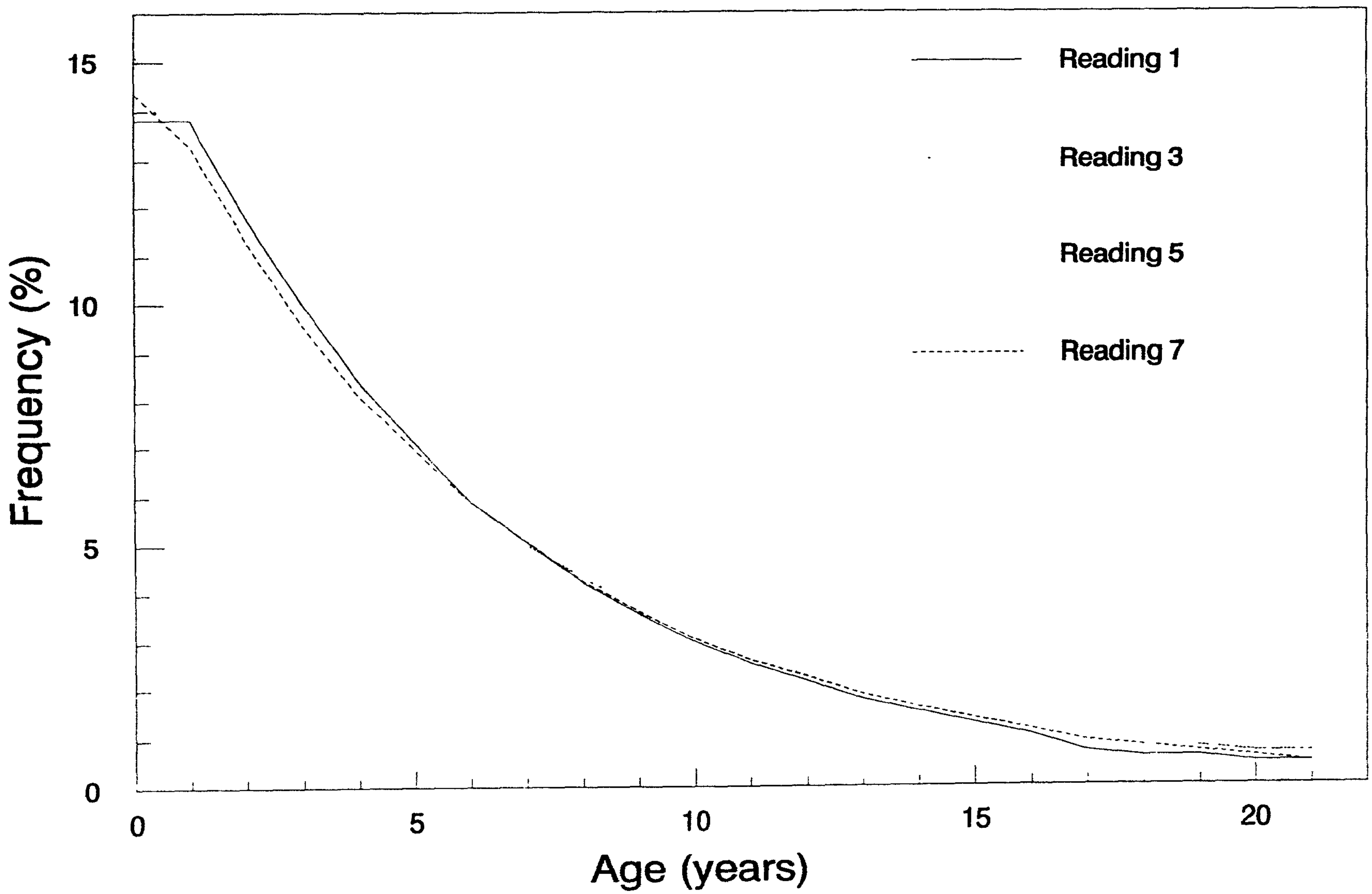
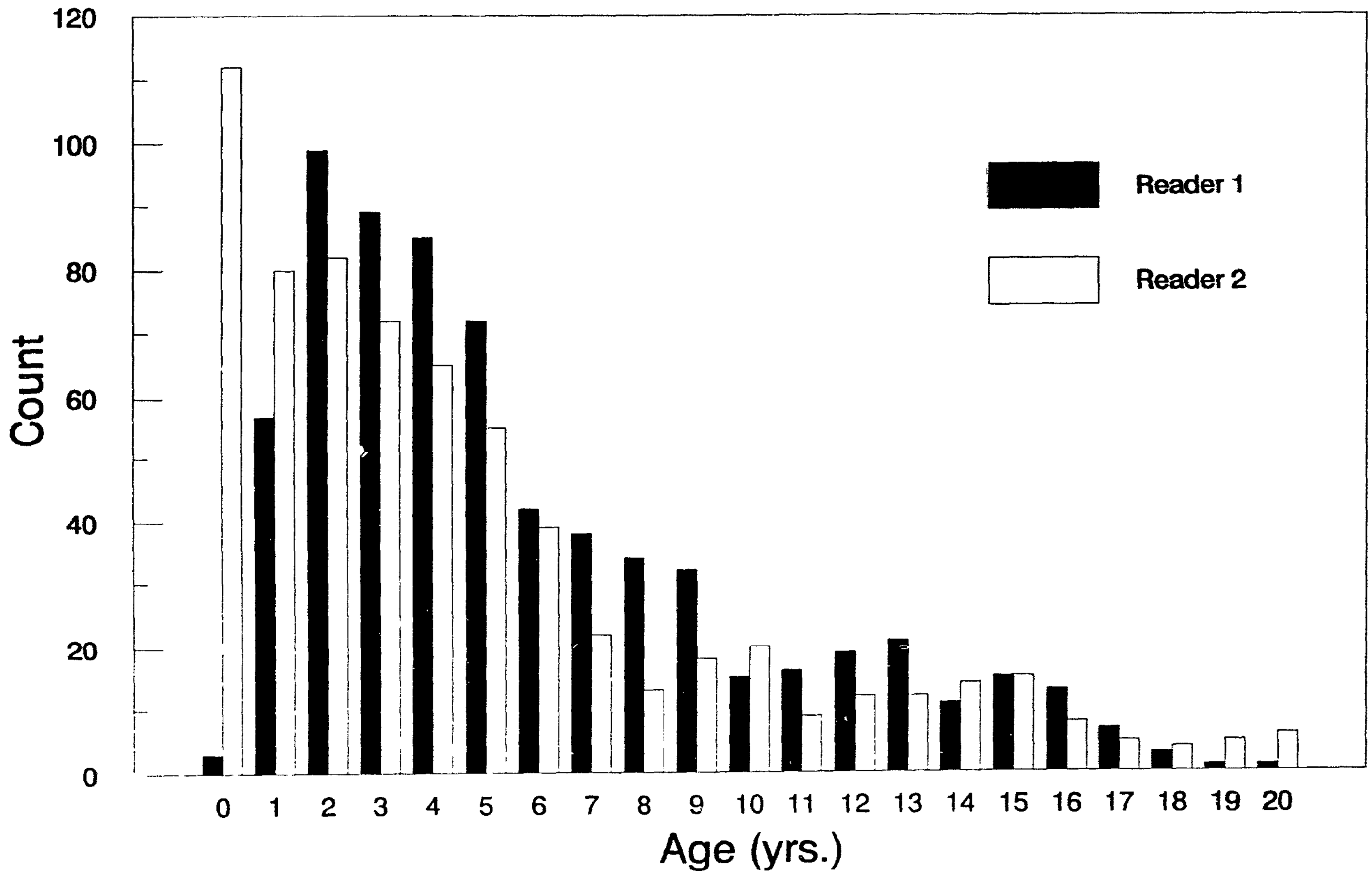

Reading 1
Reading 3
Reading 5
Reading 7
15
10
5
0
Frequency (%)
0
5
10
15
20
Age (years)

Figure 8 Age distributions from two readers. Distribution for Reader 1 is the mean of seven readings, while the distribution for Reader 2 comes from one examination of the teeth. The frequencies are significantly different (chi-square=148.1 df=20 P<0.001).



120
100
80
60
40
20
0
Count
Reader 1
Reader 2
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
Age (yrs.)

Figure 9 Stable age distribution calculated after smoothing the distributions as read by two different readers (see Figure 8).

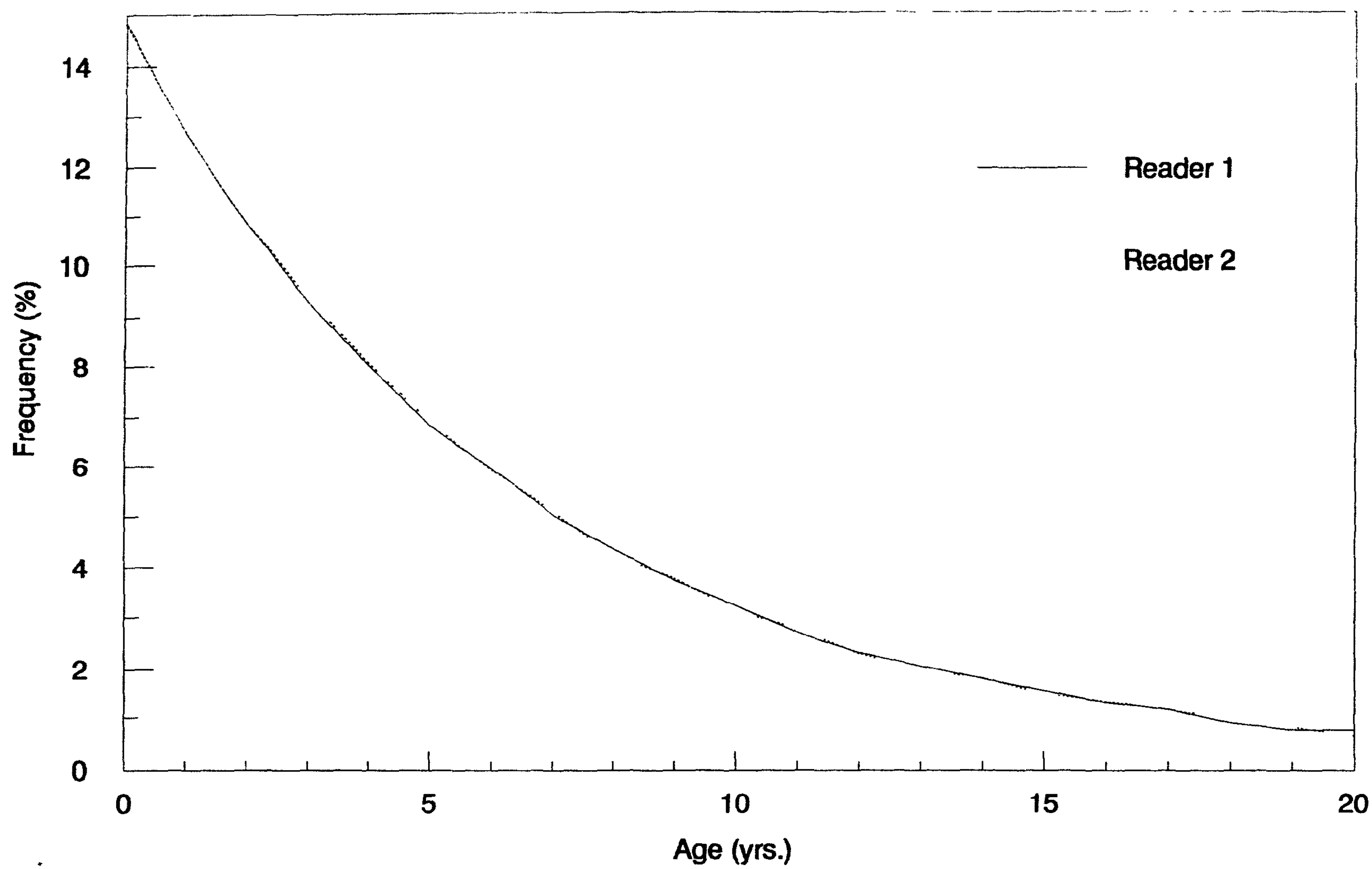
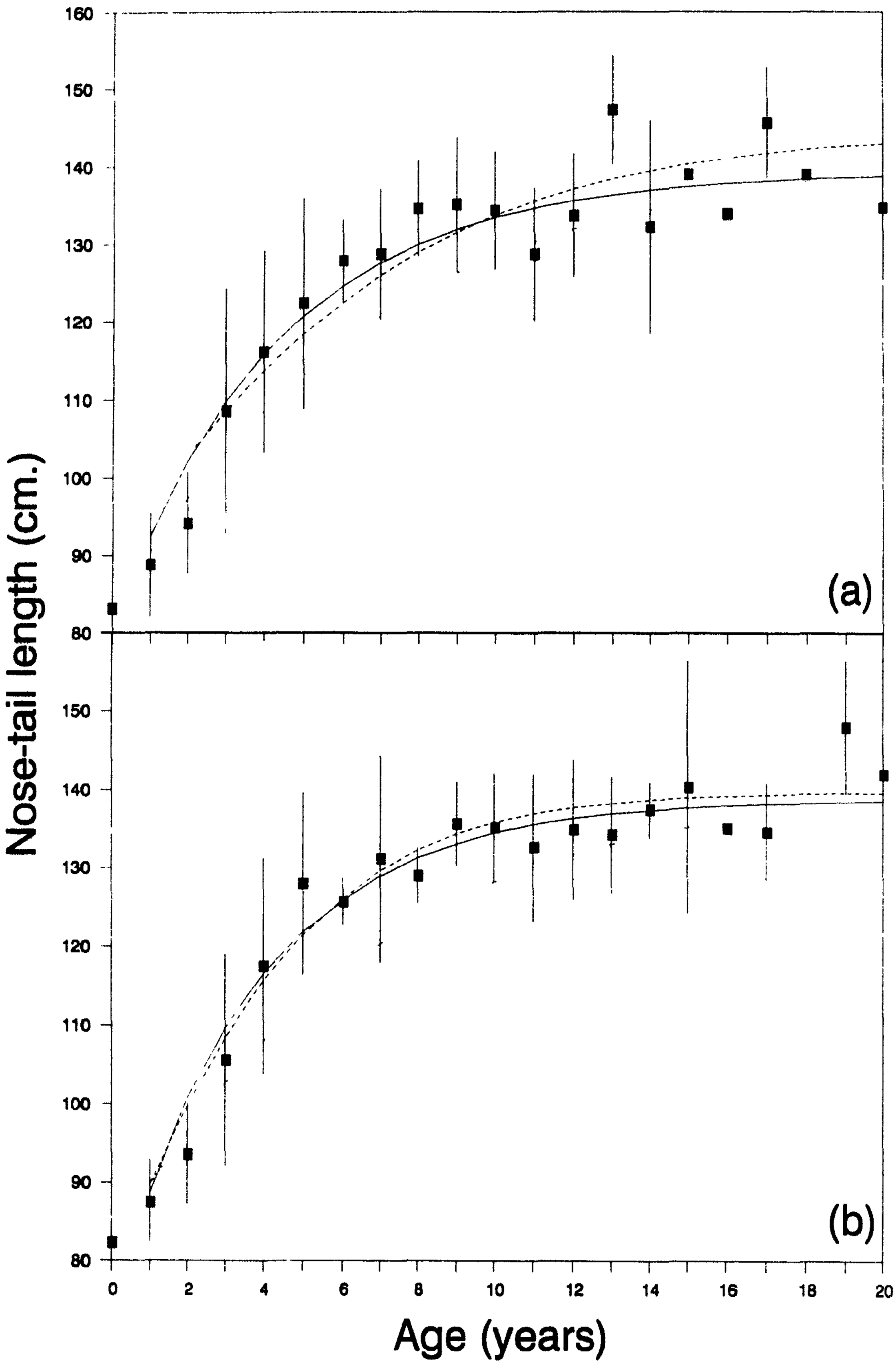

Frequency (%)
14
12
10
8
6
4
2
0
0
5
10
15
20
Age (yrs.)
Reader 1
Reader 2

Figure 10 Comparison of different growth curves for each age-class. Difference is mean absolute percentage difference (E).

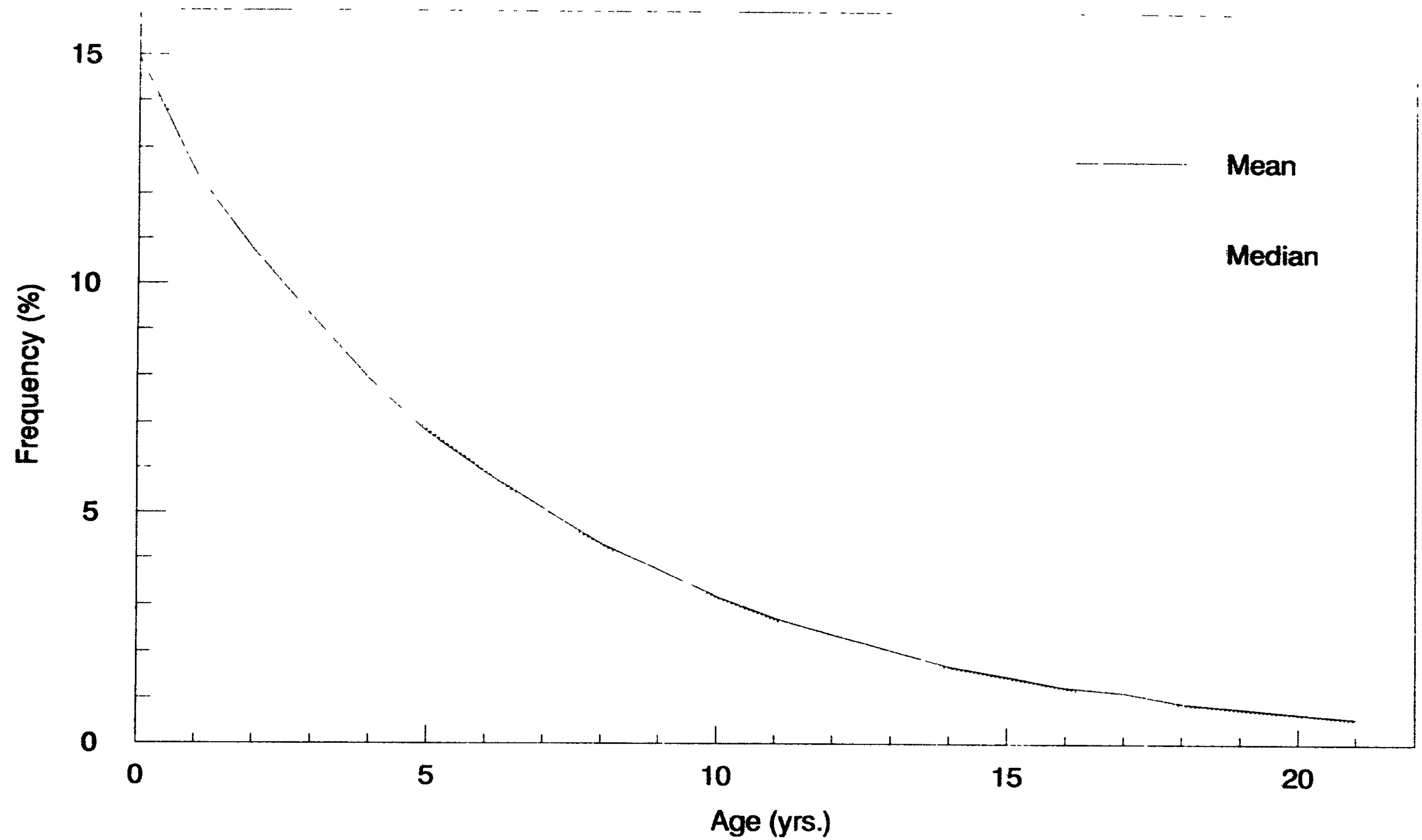
Equation	Logistic	Gompertz
von Bertalanffy		
Replicate 1	0.97	2.60
2	1.74	3.24
3	1.72	2.80
4	1.57	2.97
5	2.23	3.47
6	1.59	2.83
7	0.84	3.73
mean	0.63	2.80
Logistic		
Replicate 1		3.09
2		4.23
3		3.11
4		3.59
5		5.41
6		4.08
7		4.37
mean		2.75

Figure 11 (a) Reading 2 (b) Reading 7. Comparison of the predicted results from Gompertz (••••), logistic (- - - -), and von Bertalanffy (----) growth curves. Vertical bars represent 1 standard deviation.



Nose-tail length (cm.)
160
150
140
130
120
110
100
90
80
(a)
(b)
0
2
4
6
8
10
12
14
16
18
20
Age (years)

Figure 12 Comparison between the stable age distribution calculated using the mean and the median of seven replicate readings of Holman cross sections.



Mean
Median
Frequency (%)
15
10
5
0
0
5
10
15
20
Age (yrs.)

CONNECTING STATEMENT

Since precision and accuracy can be analyzed separately, it has been possible to consider precision without considering accuracy. Without known age animals I cannot comment on the absolute accuracy of using dental laminations for age determination in ringed seals. Section II assesses relative accuracy of the technique.

SECTION II

Accuracy of age determination in ringed seals (*Phoca hispida*)

Ringed seals (*Phoca hispida*) are small holarctic phocids. They have been important for native subsistence prehistorically (Aigner 1985) and in the modern cash economy. Ringed seals are a major prey species of polar bears (*Ursus maritimus*) and arctic foxes (*Alopex lagopus*), providing an important link between them and pelagic fish and crustaceans (Frost 1985).

Ringed seal vital parameters such as age of sexual maturity, life expectancy, and mortality rates are estimated using discrete ages determined from layering in dentine of canine cross sections (McLaren 1958; Smith 1973) and in cementum of longitudinal, stained sections (Stirling et al. 1977; Lydersen and Gjertz 1987). From analogy with similar species these age determinations were assumed accurate.

In the absence of specimens from seals of known age, comparing results from different and independent measuring processes is an indirect test of the accuracy of age determination. The rationale is that different processes arriving at similar values suggest the result is close to the true value (Mandel 1964). For the ringed seal comparisons were made of ages derived from teeth from different sides of the same animal, from different structures of teeth from the same animal, and from different readers of the same teeth.

To determine periodicity of layer formation, autoradiographs of sections of teeth collected from Svalbard in spring 1987 were made. It was hoped radioactivity from the Chernobyl nuclear accident would act as a marker in the teeth. Attempting to introduce an objective criterion that would aid both accuracy and repeatability, I measured teeth and tried to distinguish age-classes based on these measurements.

MATERIALS AND METHODS

Full details of the processing and reading of cross sections and decalcified stained longitudinal sections are given in Section I. Tooth sections were cut from the mandibular canines of ringed seals collected in Amundsen Gulf (71°N, 118°W) (Holman) and Barrow Strait (74°N, 98°W) (Resolute). Each section was read seven times without reference to biological data, using a binocular dissecting microscope with transmitted light.

Counts of the dentine in cross sections began at the neonatal line and an opaque followed by a translucent incremental growth layer (IGL; Myrick 1980) were counted as a growth layer group (GLG; Myrick 1980) (McLaren 1958; Tikhomirov and Klevezal 1964; Smith 1973). Counts of cementum in stained sections began at the cemento-dentinal interface and one light staining and one dark staining layer was considered to represent a year, as is common in many other species (Gilbert 1966; Bishop 1967; Strickland et al. 1982; and others). Cross sections were interpreted by myself (Reader 1), an experienced reader (Reader 2), and an inexperienced worker (Reader 3).

Thirty specimens collected in Barrow Strait in 1986 had lower canines identified positively as to side. Cross sections were cut and a related sample *t*-test (SAS Institute Inc. 1987: 946-947) was used to test for differences between ages from the two sides for each of the 7 readings and their mean. Kendall's τ-b (Daniel 1978: 311) was used to quantify correlation between ages from the different sides.

A number of specimens had cross sections prepared from one canine and longitudinal stained sections prepared from the other. For each of these teeth I subtracted the age derived from one structure, from the age derived from the other structure. Differences from the 7 replicates were combined and mean, SD, g_1 (skewness), and g_2 (kurtosis) (Sokal and Rohlf 1981: 114-117) of the distribution of differences were calculated for each comparison. Kendall's τ-b was used to examine correlation between ages from the different structures. Differences between readers of the same teeth were treated similarly.

The longest dimension of the opening in the root of Resolute canines was measured before they were processed. Measurements of cross sections were made without reference to ages, using an eyepiece micrometer at 12X on a Wild M5 dissecting microscope. Anterior-posterior lengths of section (S_l) and pulp cavity (P_l) were measured along the longest axis of the section (Figure 1). Labial-lingual widths of sections (S_w) and pulp cavity (P_w) were measured perpendicular to S_l at what was judged the centre of the section (Figure 1). If a piece was broken off the edge of a section not all measurements could be made. Several sections with large pulp cavities were broken so sample size was small for the youngest age-class.

From the measurements, dentine width ($D_L = S_l - P_l$; $D_W = S_w - P_w$; $D_X = [D_L + D_W]/2$) and ratios ($L = P_l/S_l$; $W = P_w/S_w$) were calculated. Univariate analysis of variance (ANOVA) and Duncan's multiple range tests were performed on PC/SAS (SAS Institute Inc. 1987) to examine the measurements and the derived values.

From seals (N = 31) collected in Svalbard (79°N, 12°E) in February to April 1987 undecalcified longitudinal sections from one canine and cross sections from the other were cut on a Buehler Isomet Low Speed Saw (Cat. No. 11-1180-170, Tech-Met Canada, 80 Milner Ave. #9, Scarborough, Ontario M1S 3P8) using High Concentration

Diamond Wafering Blades (No. 11-4244). Cross sections from harp seals (*Phoca groenlandica*) collected in the Gulf of St Lawrence in spring 1987 were used as controls. Macroautoradiography was done in cassettes made of 19 mm plywood, from the Department of Plant Science, Macdonald College. Sections were covered with aluminium foil and exposed to Kodak X-Omat AR X-ray film for 15 or 24 days. The film was developed manually (Eastman Kodak 1983).

RESULTS

The paired comparison *t*-test showed no significant difference between ages from different sides in 6 of the 8 replicate readings. A significant difference (P=0.03) occurred in one replicate while the other was marginally significant (P=0.05). Kendall's τ-b indicates high and significant correlation between sides in each case (range=0.69 to 0.82 for the readings, 0.85 for their mean; P<<0.005 in all cases). It was noted qualitative features, such as size and shape of the pulp cavity or occurrence of irregular IGLs, were similar between pairs of teeth from the same animal.

Two Kendall's coefficients were 0.49 for comparisons between Holman cross sections and readings of dentine in haemaleum stained sections. The rest were ≥0.52.

Correlations between counts from cross sections versus those from cementum of haemaleum stained longitudinal sections were between 0.60 and 0.73. Correlations for the same comparison using toluidine blue stained sections were similar (range=0.61 to 0.72).

Correlations between Resolute cross sections and toluidine blue stained sections was high (range=0.63 to 0.75). The lowest correlations from these teeth occurred between cementum and dentine readings of histological sections (one was 0.46, two were 0.47, $0.51 \leq \tau\text{-b} \leq 0.61$ for the other five). All correlations for Holman and Resolute teeth were highly significant ($P \ll 0.005$).

Correlation between readers was also consistently high (Figure 2). One Kendall's coefficient between Reader 1 and Reader 2 was 0.62 while the others were between 0.70 and 0.78. The lowest correlation between Reader 1 and Reader 3 for Resolute teeth was 0.73, based on 14 observations. Kendall's τ-b for 3 other replicates of 48 teeth and their mean ranged between 0.85 and 0.89. Again all correlations were highly significant ($P \ll 0.005$).

A weakness of using Kendall's τ-b in this situation is that correlation may be strong even though one member of each pair is consistently higher than the other. Counts of dentinal IGLs from cross sections tended to give higher ages than either cementum or dentine in stained longitudinal sections (Table 1) as shown by the significant mean difference and positive skewness. The difference between age from readings of dentine and cementum in Holman histological sections was not significantly different from 0 nor was the distribution skewed. On the other hand, differences in readings between cementum and dentine of the Resolute sections were significantly different from 0 and had a negative skew. Reader 1 tended to assign a lower age than either of the other readers. All distributions had significant leptokurtosis meaning there was a peak around the mean difference.

All seals with root canal openings > 1.8 mm had a mean age of 0 (N = 13 cross sections, 6 stained sections). One-way ANOVAs showed significant differences (Table 2) in dentine and pulp cavity measurements between age-groups determined by counting dentinal GLGs in cross sections. However Duncan's test revealed overlap between several consecutive age-classes in all cases (Figure 3). Sorting measurements by sex did not alter the results.

Of 58 sections from ringed seals and 17 sections from harp seals only 1 showed any sign of activity in the autoradiographs. This result could not be duplicated in a subsequent run with more sections cut from the same tooth.

The one image that did appear, showed radioactivity on the outside of the tooth rather than in the dentine near the pulp cavity.

DISCUSSION

If different teeth from the same animal, different structures from the same animal, or different readers of the same teeth arrive at similar values, it suggests read age is representative of true age. Considering the variability of age determination between readings of the same tooth (Section I), perfect agreement in ages under these conditions could not be expected.

The paired sample *t*-test showed ages from each side of the same animal were not significantly different. The single instance of a significant difference can probably be attributed to chance, because of the small number of replicates. Strong correlation shown by Kendall's τ-b indicates a tendency for higher ages from different sides to be paired together. While this is not proof of absolute accuracy, it suggests relative accuracy in age determination from teeth.

Surprisingly few studies have examined different teeth from the same animal for correlation between estimated age. Phillips and Steinberg (1976) found wide variation in the number of cemental layers of various teeth from the same vampire bat (Desmodus rotundus). Conversely, McCullough and Beier (1986) noted good agreement between ages from upper and lower teeth of deer (Odocoileus spp.). These two studies and my study all have small sample sizes. However, qualitative observations made while reading these teeth lead me to believe the same factor is influencing canine growth from the same animal equally. While estimated age will be slightly different between sides, there is general agreement between ages from different sides.

High correlation between dentine and cementum from the same animal suggest read age is representative of true age. In this study significant correlation occurs between ages from cementum and dentine whether the dentine was read in cross or in longitudinal sections. Consistency between structures strengthens the notion the age estimates reflect true age of the animal.

The lowest correlations occurred between dentine and cementum of stained sections, whether the stain was haemaleum or toluidine blue. Although Alaskan workers routinely examine dentine in stained sections (K. Frost, Alaska Dep't. Fish Game, 1300 College Rd., Fairbanks, AK.

99701, pers. commun.), I found it less distinct than cementum in stained sections. This difference in clarity of GLGs probably contributed to the lowered correlations.

Another factor which would affect correlation between cementum and dentine in stained sections is the placement of the cementum on the tooth. First year cementum is not laid down along the entire length and it may have been overlooked in some readings.

Kendall's τ-b between readers was consistently high and significant. Again this suggests the age arrived at by different readers of the same teeth bears some resemblance to reality when each reader determines the same teeth to be young and the same teeth to be old.

There are undoubtedly some problems with absolute accuracy of certain teeth. Bowen et al. (1983) show inaccurate estimates may be made consistently while determining age of harp seals from cross sections. A few ringed seal teeth gave consistent ages that made no sense when compared to other data collected e.g. reproductive state or size of the animal. Such cases might be blunders made while recording data or processing the tooth. Thickness, eveness, and angle of the section with regard to GLGs may affect accuracy of the count by hiding IGLs or distorting their widths.

Measurements

Overlap between age-classes for section length (S_l) and section width (S_w) show canines are fully developed early in life. Deposition of dentine, measured by pulp length (P_l), shows the expected pattern as the seal ages i.e. amount of dentine increases. However deposition is so slow age categories overlie each other. Overlap is large enough that not even broad age categories can be discerned. Jean et al. (1986) obtained similar results for coyotes.

Specimens in this study were not of known age, so mistakes in age classification certainly occurred because of error inherent in the technique of counting GLGs. A large number of known age animals would be necessary for further work. Tooth abnormalities may affect the results. In arctic foxes there is variation in measurements of L between the canines of the same animal, with marked divergence if one of the canines has been damaged (Grue and Jensen 1976). This is probably not an important factor considering the sample size here, at least in most of the younger age-classes.

In some terrestrial fur-bearing species (e.g. marten (*Martes americana*); Dix and Strickland 1986; Nagorsen et al. 1988) animals less than 1 year old can be separated from older animals on the basis of measurements of radiographic images. This saves time and expense by excluding these teeth before histological processing. It appears openness of the root canal can be used to quickly separate young of the year from older age-classes of ringed seals. Older animals may have a small opening for the passage of blood vessels or nerves, but distinction should be relatively simple.

Smith (1973) puts closure of the root canal in ringed seals between the ages of 2 and 3 years. His figure 3 illustrates a 2+ year old animal with a small root canal opening, but he did not have known age animals. Bowen et al. (1983: Figure 2) found canal width was ≥ 2.0 mm in harp seals collected during the first half year of life. However animals up to 3.5 years had root canals of similar dimensions. My sample was collected in spring and early summer soon after the birth period. It may be more difficult to accurately sort age-classes of samples collected during late winter or just previous to seals achieving their first birthday.

Because counting GLGs in ringed seal teeth is a subjective matter, objective criteria to aid in age determination are desirable. However, measurements of tooth cross sections do not give unequivocal classifications. Size of pulp cavity and dentine thickness may be used as a subjective check on accuracy of the count of layers but they cannot be used by themselves in age determination.

Marking Animals

The attempt to use Chernobyl radiation as a marker to distinguish layers was a failure. Autoradiography initially detected the Chernobyl radiation cloud (Devell et al. 1986) and has been used to monitor its spread (Druehl et al. 1988). There are three reasons for failure in this application. First, radiation was deposited in irregular, localized patches and what fell in the oceans sank to the benthos in a matter of days (Kempe and Nies 1987). Second, the radionuclides (Whitehead et al. 1988) were not species that would be deposited in teeth. Third, short half life of the radio isotopes (Mitchell and Steele 1988) may have made detection impossible.

To verify accuracy of age determination, known age animals are necessary. Tagging studies, with their low rates of return for ringed seals (Smith 1987) would require an economically unfeasible effort to validate all age-classes (Beamish and McFarlane 1983). Use of tetracycline (Gurevich et al. 1980; Beamish and Medland 1988; and others) seems most appropriate, at least to test the annual nature of GLGs. Problems of recapturing marked ringed seals are great, but some animals in Svalbard have been marked. If they can be collected in the future they will provide a test of the assumption of annual deposition of layers.

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Table 1 Differences between repeated readings of the same teeth. g1 is a measure of skewness, g2 is a measure of kurtosis, N is the total of the repeated readings. For Reader 1 vs. Reader 3 divide N by 4 to get the total number of animals; for others divide N by 7.

Comparison	Mean Difference	SD	g1	g2	N
1981 Holman					
(Cross section age)-(Cementum age+)	2.25***	2.99	0.54***	7.20***	856
(Cross section age)-(Dentine age+)	1.98***	2.73	0.54***	2.79***	865
(Cementum age)-(Dentine age+)	-0.17	2.78	-0.11	18.62***	927
(Cross section age)-(Cementum age++)	3.00***	3.58	1.76***	3.85***	296
(Reader 1 age)-(Reader 2 age)	-1.34***	2.91	-1.29***	7.46***	276
1984 Resolute					
(Cross section age)-(Cementum age++)	1.19***	2.76	-0.02	2.62***	193
(Cross section age)-(Dentine age++)	1.28***	3.47	3.03***	16.79***	333
(Cementum age)-(Dentine age++)	1.00***	4.31	-0.61***	2.23***	474
(Reader 1 age)-(Reader 3 age)	-1.09***	1.89	-0.37	2.10***	155

+ haemaleum stain ++ toluidine blue stain

*** P<0.001

Table 2 Results from ANOVAs comparing tooth measurements between ages (0-29 years) estimated from counts of growth layer groups. For explanation of measurements see text.

	F-value	Prob.'	N
S_1	1.62	<0.05	542
S_w	2.66	<0.01	584
P_1	57.82	<0.01	597
P_w	52.32	<0.01	601
D_L	106.75	<0.01	541
D_W	66.35	<0.01	584
D_X	91.19	<0.01	526
L	91.67	<0.01	541
W	70.95	<0.01	584

Figure 1 Section length (S_l; between open arrows) was measured along the longest axis of cross sections as was length of the pulp cavity (P_l; dashed line). Section width (S_w; between solid arrows) and width of pulp cavity (P_w; dotted line) were measured perpendicular to S_l at what was judged the middle of the section.

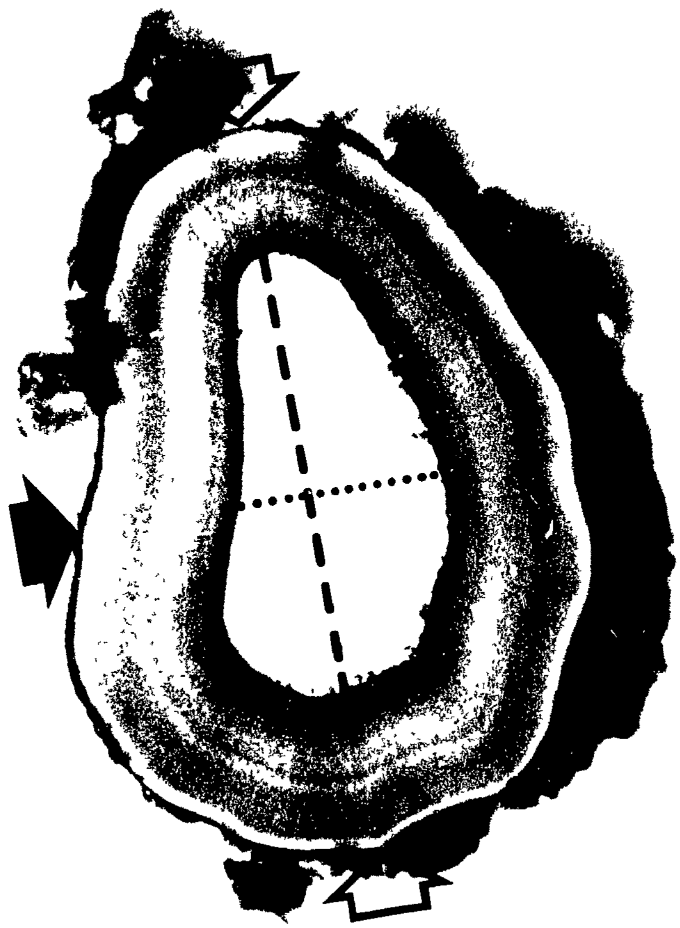

Figure 2 Comparison of mean age from 7 readings of Holman cross sections for each of 2 readers. Line indicates 1:1 correspondence of mean age between readers. Kendall's τ-b=0.78 ($P<<0.005$).

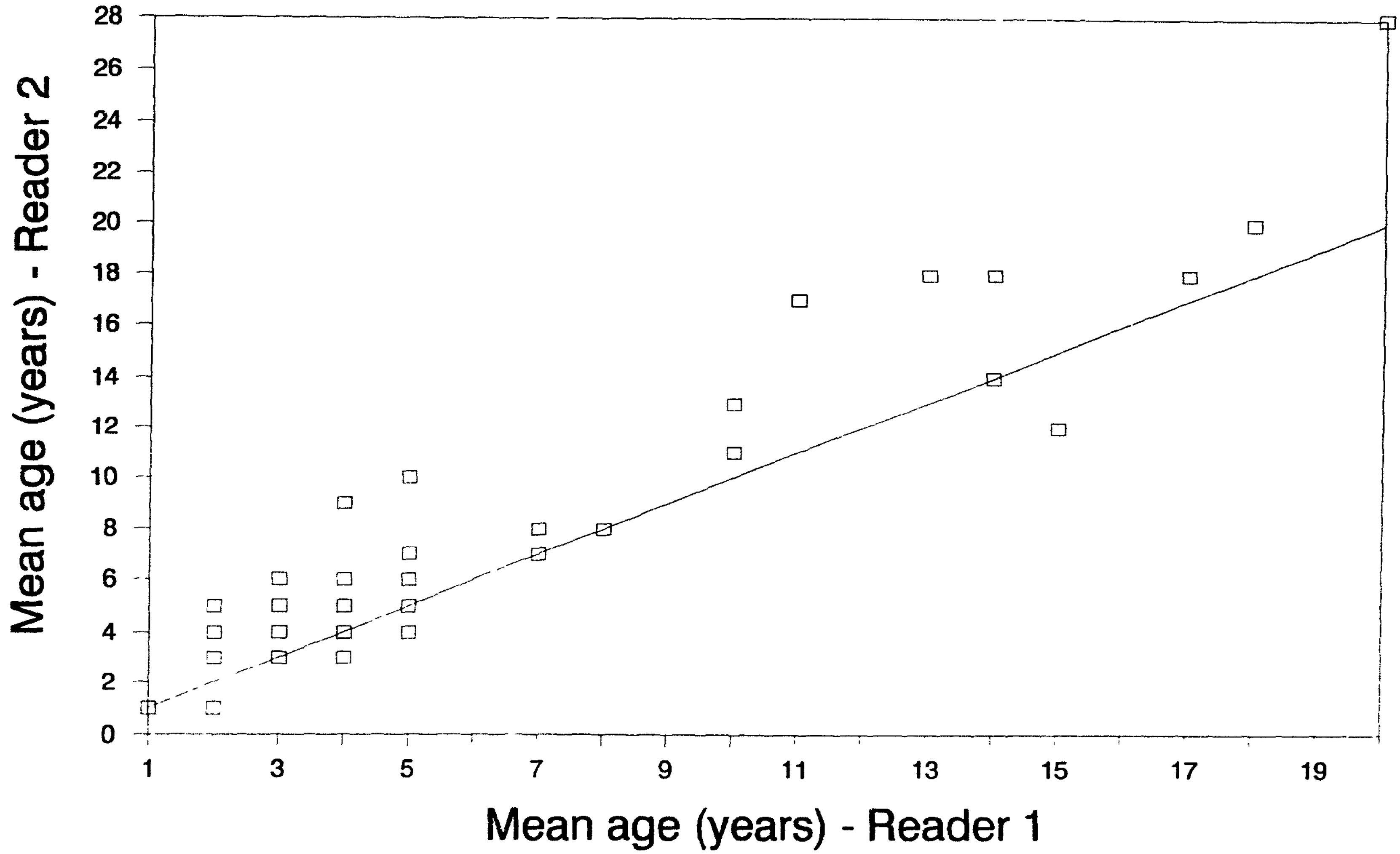
Mean age (years) - Reader 2
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
1
3
5
7
9
11
13
15
17
19
Mean age (years) - Reader 1

Figure 3 Typical results from Duncan's multiple range test for section length (SECTL), length of pulp cavity (PULPL), and SECTL/PULPL (LRATIO) of ringed seal canines. Means with a common underline are not significantly different (P=0.05). Means are in eyepiece micrometer units (1 epu=0.83 mm).

a. SECTL

n	1	1	2	2	1	1	4	58	63	13	1	1	10	17	62	44	13	58	40	9	21	7	30	33	15	3	30	2
Age	27	18	20	21	29	22	17	4	5	15	28	19	16	12	3	1	14	2	6	10	13	0	7	8	11	23	9	25
Mean	10.2	9.0	8.8	8.7	8.7	8.3	8.3	8.2	8.2	8.2	8.1	8.1	8.0	8.0	8.0	8.0	8.0	7.9	7.9	7.9	7.9	7.9	7.8	7.8	7.8	7.6	7.6	7.6

b. PULPL

n	45	6	62	66	64	65	41	34	33	38	14	2	19	1	18	27	17	14	13	5	2	2	1	3	2	1	1	1
Age	1	0	2	3	4	5	6	7	8	9	10	18	12	19	11	13	14	16	15	17	20	21	29	23	25	22	28	27
Mean	6.5	6.3	6.2	5.9	5.5	5.3	4.9	4.3	4.0	3.2	2.9	2.4	2.3	2.3	2.2	2.2	2.1	2.0	1.6	1.4	1.4	1.2	1.1	0.7	0.6	0.3	0.3	0.3

c. LRATIO

n	44	6	58	62	58	63	40	30	33	30	1	9	17	21	15	1	13	10	13	4	2	2	1	3	2	1	1	1
Age	1	0	2	3	4	5	6	7	8	9	18	10	12	13	11	19	14	16	15	17	20	21	29	23	25	28	22	27
Mean	.80	.79	.79	.75	.68	.64	.62	.55	.50	.43	.41	.39	.29	.29	.28	.28	.27	.24	.19	.17	.15	.13	.13	.10	.08	.04	.04	.03

CONCLUSION

This is quality control work in a sense. It relates to the precision of determining age of ringed seals from tooth structures and the effect this precision has on perceptions of the population dynamics. Since this work was meant to simulate applied aspects of age determination for management purposes certain techniques, e.g. electron microscopy and amino acid racemization, are not practical because of cost or time constraints. This work relied on standard procedures of sectioning undecalcified teeth and histological preparations of decalcified teeth.

Lack of clarity and contrast of dentinal incremental growth layers (IGLs) in undecalcified cross sections cause problems for repeatability and accuracy. In cementum of stained sections, width of layers and joining and splitting of the layers affect repeatability and accuracy. Both cross sections and histological sections give similar levels of repeatability. Absolute accuracy can not be judged.

No differences were found in repeatability between sexes or between sides from the same animal. Thus large samples can be lumped without regard to sex and paired comparisons can be made between dentine and cementum from different canines of the same individual.

Evidence from this work, from descriptions in the literature, and from a number of other species suggest geographical differences in repeatability of age determination occur. Thus age determined for animals from some areas may have more uncertainty involved.

There is no apparent difference in repeatability between haemaleum and toluidine blue stains. Although toluidine blue results in sections which seem easier to interpret, its use can not be justified on the grounds of repeatability among readings.

Difference in levels of precision between readers may not be as great as it appears to be. Readers 1 and 3 had similar levels of precision. Reader 2's greater precision may have been because he read the teeth over a short length of time. Regular practice seems necessary for achievement of high levels of repeatability.

Other techniques e.g. machine reading are available which would appear to be more precise than subjective interpretation by peering through a microscope. However observations of IGLs in cross sections changing opacity with alteration of the angle of the reflecting mirror or of the section's orientation to the mirror suggests machine reading would not be as repeatable as expected. Nor would machine reading necessarily make readings more accurate. Widths of IGLs are probably not consistent enough among teeth to be used as a criterion. In any case known age animals would be necessary for calibration.

Ages can be used in one of two ways. They may be entered into a frequency where other characteristics are not important, e.g. the mean age of a population, or they may be used to group individuals for which some other characteristic is of interest e.g. occurrence of sexual maturity.

Reading the same set of teeth repeatedly results in mean ages that are statistically different. Variation in age determination is only one possible source of error affecting the mean age, but it alone can give an incorrect perception of difference between two populations. Similarly, calculations of mean age of sexual maturity are affected enough by variation in age determination to identify repeated readings of the same sets of teeth as being from different populations.

On the other hand, neither life tables and Leslie matrices nor growth curves are affected by differences between readings. This is good from the point of view that the same results will be obtained despite variation in age determination. However it points to the lack of sensitivity of the methods to real differences between populations.

Age reading of seals older than 12 years are little more than random numbers. For the parameters I examined this does not seem to have much import. When dealing with frequencies rather than individuals, there are relatively few seals of these ages. Seals of these ages are above the age of sexual maturity so they do not enter into calculations of this statistic. For growth curves, seals of this age are near the asymptotic length so here again changes in the placement of an individual will not affect the final results. It should be possible to lump older seals into age classes which span 5 or 10 years without any particular loss of information.

Without known age animals no definite statement can be made about accuracy of determining age from ringed seal teeth. However correlation between teeth from different sides of the same animal, between dentine and cementum of the same animal, and between readers examining the same teeth suggests read age is representative of true age. Nonetheless there was a small number of animals whose age was determined consistently, although it made little sense when compared to other available data. Gross levels of inaccuracy would destroy the value of this technique for management decisions. It appears the technique, while inaccurate for a small percentage of individuals, is accurate enough to allow management recommendations to be made.

A problem with the measures of imprecision used here is that they are ratios and are affected by the age distribution. Someone who reads teeth consistently older than another person will almost certainly appear to have greater precision. Thus, known age animals are necessary to evaluate both precision and accuracy. A large sample of known age animals would involve a massive tagging effort and an even more massive recapture effort. Such a project would be prohibitively expensive. For the present we need to be cognizant of the variation in age determination and the effect it can have on estimates of various parameters. Age determination of ringed seals, and indeed all animals, would benefit from consultation between the various workers to standardize their methodologies.

GLOSSARY

Accuracy - The closeness of a measured value to the true value.

Ageing (or aging) - A verb which means to make old or mature (Spinage 1973).

Bias (=systematic error=constant error) - A consistent difference between the measured value and the true value (Hamaker 1986) caused by technique or tools (Hunter and Priest 1960). Presence of bias affects accuracy of a result in a certain direction (Hamaker 1986).

Cementum (Figure 1) - A calcified tissue of mesodermal origin, often containing osteocytes (cementocytes) and forming layers over the root and in some species, over part of the coronal portion of a tooth. Serves as `attachment bone´ of the tooth (Myrick 1980: 48).

Crown (Figure 1) - The coronal (or distal) part of a tooth that in life protrudes from the gingival surface and that is demarcated by an enamel covering in most species (Myrick 1980: 48).

Dentine - Acellular, calcified tissue of mesodermal origin that constitutes most of the tooth body (root and crown). It is covered on the crown by enamel and basally by cementum (Myrick 1980: 48).

Discrepancy - The difference between two measured values of a quantity (Hunter and Priest 1960) e.g. the difference between age, as determined by two investigators, from the same tooth (v. reproducibility, repeatability).

Enamel (Figure 1) - Acellular (prismatic) highly mineralized secretion of ectodermal origin forming an external covering for the dentine. May be itself in part covered with cementum (Myrick 1980: 48).

Error - The difference between a measured value and the true value. Except in a few cases, the true value is unknown and the magnitude of the error is hypothetical (Hunter and Priest 1960: 405) (cf. mistake).

Experimental (=accidental=erratic) error - The difference between the values when a given measurement is repeated (Hunter and Priest 1960).

Gingival - Of or pertaining to the gums.

Growth layer group (GLG) (Figure 1) - A repeating pattern of groups of incremental growth layers (q.v.) which may be recognized by virtue of cyclic repetition, generally at constant or regularly changing relative spacing in the characters delineating the layers. Such a cyclic repetition of incremental growth layers must involve at least one change (e.g. between translucent and opaque, dark and light, more stained and less stained), but may involve more than one change. The number of incremental growth layers forming a growth layer group must be determined for each species (Lockyer et al. 1980: 2).

Incremental grcwth layer (IGL) - A discernible layer parallel to the formative surface of a hard tissue (cementum, dentine, bone) which contrasts with adjacent layers (Myrick 1980: 49). The contrasting nature may be:

a) translucency and opacity of a section examined using transmitted light

b) dark and light layers seen under incident (reflected) illumination

c) more or less intense staining of a decalcified, cut surface where basic stains are most commonly used (Lockyer et al. 1980).

In cross sections IGLs are arranged more or less concentrically around the pulp cavity (Hohn 1980). Also referred to in the literature as `bands´, `laminae´, `lines´, `zones´, (Lockyer et al. 1980: 2) and, `annuli´. `Rest lines´ and `winter lines´ in cementum of stained sections relate to the narrow, darkly stained IGLs.

Mistake - A blunder for which no systematic treatment of error can cope (Hunter and Priest 1960) e.g. mislabelling of teeth and clerical errors (e.g. accidental omission or inversion of digits) (cf. error).

Neck (Figure 1) - The region of a tooth immediately below the enamel that separates the anatomical crown from the root (Myrick 1980: 49).

Neonatal line (Figure 1) - A particularly well defined growth layer separating prenatal dentine from postnatal dentine. It is believed to be a product of disturbances of the perinate's nutrition in the immediate post-partum period (Myrick 1980: 49).

Occlusion of pulp cavity - The condition in which the pulp cavity has become filled with dentine, and/or primary dentinal accumulation has ceased (Myrick 1980: 49).

Opaque incremental growth layer (OIGL) (Figure 1) - Appears dark in transmitted light and light in reflected light (Lockyer et al. 1980: 2).

Periodontal membrane (ligament) - Connective tissue containing collagenous fibers that pass from the cement of a tooth to the lamina dura of the tooth socket (Myrick 1980: 49).

Precision - The variability of repeated test results (Hamaker 1986) (v. repeatability, reproducibility).

Pulp cavity (Figure 1) - The central conical or cylindrical chamber of a tooth bounded by dentine which, in life, contains the pulp consisting of connective, sensory, and nutritive tissues (Myrick 1980: 49).

Repeatability - The variability of repeated results from a single observer (Hamaker 1986) (cf. reproducibility).

Reproducibility - The variability of results from different observers (Hamaker 1986) (cf. repeatability).

Root (Figure 1) - That part of a tooth typically covered by cementum and contained within the tooth socket below the gingival surface (Myrick 1980: 50).

Translucent incremental growth layer (TIGL) (Figure 1) - Appears clear or light using transmitted light and dark under reflected light (Lockyer et al. 1980: 2).

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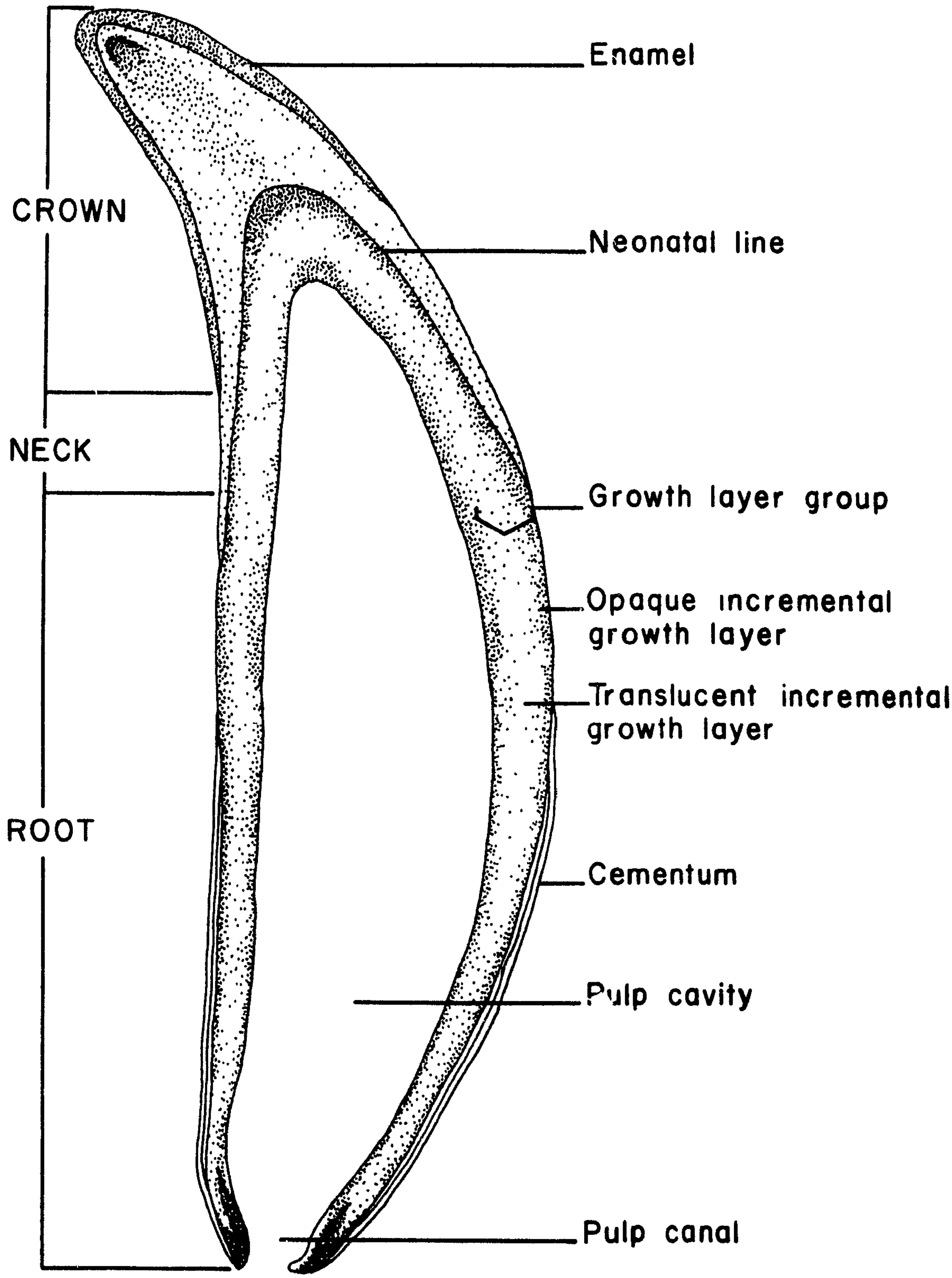
Figure 1 Illustration of terms in the glossary.



CROWN
NECK
ROOT
Enamel
Neonatal line
Growth layer group
Opaque incremental growth layer
Translucent incremental growth layer
Cementum
Pulp cavity
Pulp canal